Genetic and environmental underpinnings of educational achievement at the end of compulsory education and beyond

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Abstract

Educational achievement is of major societal interest and is crucial to students themselves, as academic achievement during compulsory education propels young individuals to different life-long trajectories. Research has shown that individual differences in educational achievement are to a substantial extent (around 60%) explained by inherited differences in children's DNA sequence. However, most of the research to date has focused on reading and mathematics achievement during primary school education. Much less is known about the genetic and environmental underpinnings of educational achievement in secondary school across the various subjects children study. Furthermore, even less is known about educational achievement after compulsory education. It is imperative to understand why individuals differ so widely in educational achievement, to understand the causes and correlates of scholastic achievement and to inform evidence-based educational policy.

The current project seeks to increase understanding of the aetiology of individual differences in educational achievement at the end of compulsory schooling and beyond. This thesis explores the genetic and environmental underpinnings of educational achievement in the UK, focusing on achievement at the end of compulsory education, and educational attainment in Estonia. I use data from the UK representative Twins Early Development Study (TEDS), and the Estonia representative adult sample from the Estonian Genome Centre University of Tartu (EGCUT), to investigate the following: the aetiology of educational attainment during the Soviet occupation and post Soviet era in Estonia (Chapter 2); the relationship between first and second language achievement, and general cognitive ability (Chapter 3); the proportion of heritability of educational achievement that can be explained by cognitive and non-cognitive factors at age 16 (Chapter 4); the prediction of exam results from personality (Chapter 5); and the aetiology of subject choice after compulsory education, and achievement in these chosen subjects at age 18 (Chapter 6).

The thesis provides evidence that i) genetic factors explain a larger proportion of educational attainment in a more meritocratic society, where selection to educational and occupational positions is based more on merit and ability than environmentally-driven privilege; ii) educational achievement in second language learning is highly heritable and this high heritability is only partly explained by first language achievement and intelligence; iii) the high heritability of academic achievement is explained by non-cognitive as well as cognitive factors; iv) the popular concept of Grit (perseverance and passion for long-term goals) adds little to the prediction of exam performance beyond the 'Big Five' personality factors; v) genetics affects both aptitude (cognitive ability) and appetite (subject choice) for learning. I conclude the thesis with a discussion about implications of the work and suggestions for future directions (Chapter 7).

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Author declaration

Data used in the thesis from the Estonian Genome Centre University of Tartu (EGCUT) and the Twins Early Development Study (TEDS) were collected prior to the research described here. I was responsible for preparing the phenotypic and genetic data for the analyses and was responsible for all analyses conducted. To the best of my knowledge, the work presented here is original and my own work, except where acknowledged in the text.

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Chapter 1: Introduction

Background

Compulsory education is one of the most expensive early environmental interventions, costing around 6% of GDP (gross domestic product) (Organisation for Economic Co-operation and Development (OECD), 2013). Educational achievement is important to society and to children as individuals. Compulsory education in the UK culminates with standardized nation-wide exams, the GCSEs (General Certificate of Secondary Education). GCSE grades constitute a gateway to further education, university acceptance and even later employment, shaping individuals' life-long educational and professional trajectories. School achievement has been shown to be a good predictor of life outcomes from occupational status and potential earnings to wellbeing, happiness, health and even life expectancy (Arendt, 2005; Cutler & Lleras-Muney, 2012; Furnham & Cheng, 2016; Gottfredson, 1997; Oreopoulos & Salvanes, 2011). Therefore, it is imperative to understand the causes and correlates of individual differences in scholastic achievement, so that we move towards evidence based educational policy to improve school achievement and to ensure that every child achieves their maximum potential.

There is now converging evidence for heritability of educational achievement across school years using family designs, such as twin and adoption studies, but also DNA based methods. Twin studies have shown that around 60% of individual differences in school achievement are explained by inherited differences in children's DNA sequence (Bartels, Rietveld, Van Baal, & Boomsma, 2002; Coventry et al., 2012; Kovas, Haworth, Dale, & Plomin, 2007; Krapohl et al., 2014; Petrill et al., 2010; Rimfeld, Ayorech, Dale, Kovas, & Plomin, 2016; Rimfeld, Kovas, Dale, & Plomin, 2015; Shakeshaft et al., 2013; Wadsworth, DeFries, Fulker, & Plomin, 1995; Wainwright, Wright, Geffen, Luciano, & Martin, 2005). There is evidence for high heritability of educational achievement in the UK (Kovas et al., 2007; Rimfeld et al., 2015; Shakeshaft et al., 2013), in Sweden (Lichtenstein, Pedersen, & McClearn, 1992), in the Netherlands (Bartels et al., 2002), in Australia (Baker, Treloar, Reynolds, Heath, & Martin, 1996; Wainwright et al., 2005) and in the US (Hart, Petrill, Thompson, & Plomin, 2009; Petrill & Wilkerson, 2000) to name a few. An interesting facet of this substantial heritability is that the estimates vary somewhat across these developed Western countries (Samuelsson et al., 2005). The possible explanation for this could be the educational curriculum, with higher heritability noted in countries where educational curriculum is standardized, such as in the UK. Heritability (including SNP heritability) refers to the proportion of individual differences that can be explained by inherited differences in individuals' DNA sequence in a particular population at a particular time; it describes what is, not what could be (Krapohl et al., 2014; Shakeshaft et al., 2013). With major changes in a population or in the environment the estimate of heritability could change drastically. If all environmental differences were attenuated then there would still be differences between individuals in a population, for example in educational attainment or occupational status; so decreased environmental variance would increase the heritability estimate as a larger proportion of individual differences would be explained by genetic factors (Knopik, Neiderhiser, DeFries, & Plomin, 2017; Krapohl et al., 2014; Shakeshaft et al., 2013). If this is true, then the heritability of educational attainment could be considered as an index of equal opportunity in a society (Shakeshaft et al., 2013).

Heritability of educational attainment has been shown to vary according to birth cohort, or sex (Branigan, Mccallum, & Freese, 2013) or following an educational reform (Okbay et al., 2016). Higher heritability has been noted in countries where educational curriculum is highly standardized, such as the UK, this could be because the standardization reduces environmental differences between schools (Samuelsson et al., 2005). However, research so far have yielded mixed results, with some studies showing change in heritability estimates following a change in curriculum, or changes in the heritability of achievement across birth cohorts, and other studies not showing such an effect (Baker et al., 1996; Branigan et al., 2013; Colodro-Conde, Rijsdijk, Tornero-Gómez, Sánchez-Romera, & Ordoñana, 2015). The major limitation to date is that most research has been done in Western countries and many studies have been greatly underpowered.

The work presented in the present thesis extends the work done to date to investigate how heritability of educational attainment changes following a massive social change by using data collected in Estonian Genome Centre, University of Tartu (EGCUT) - a representative sample of more than 12 000 Estonians. Estonia was occupied by the Soviet Union after the World War II and regained independence in 1991, when there was an abrupt change from communism to capitalism. This allows us to study the extent to which this social change can affect the aetiology of educational attainment and occupational status.

Previous studies have shown that educational achievement is highly heritable from very early on in development, from early reading and literacy skills in preschool (Kovas et al., 2007; Petrill, Deater-Deckard, Thompson, Dethorne, & Schatschneider, 2006; Selzam, Dale, et al., 2017), to more formal education in primary school and middle school (Davis et al., 2014; Davis, Haworth, & Plomin, 2009a; Kovas et al., 2007), extending to the end of compulsory education (Shakeshaft et al., 2013). The interesting facet about the behavioural genetic studies is that the heritability of early achievement is even stronger than the heritability of intelligence, even though it is often assumed that the high heritability of school performance is explained by the heritability of general cognitive ability (Kovas et al., 2013). However, most of the research in educational achievement has focused on English and mathematics, and much less is known about the aetiology of educational achievement across the range of subjects children study at school. The work I did during my Masters (MSc) year extended this research studying the aetiology of GCSE results across the range of academic subjects children study at school. We hypothesized that subjects that involve more than just factual knowledge, and therefore could be more closely related to intelligence, would show higher heritability compared to more factual based subjects, such as history or geography; and more creative subjects such as art and music. We demonstrated that educational achievement is highly heritable across the subjects children study at school, and the aetiology of achievement is very similar across school subjects. We also demonstrated that this high heritability was not explained by intelligence alone, as the heritability estimates did not differ significantly when we controlled for intelligence in the analyses (Rimfeld et al., 2015).

Multivariate genetic analyses (see methods) allows us to extend the univariate design to study the covariance of traits, for example the stability of educational achievement and the causes and correlates of different types of scholastic achievement. Twin studies have shown that educational achievement is highly heritable with similar heritability estimates obtained across school years, indicating that there are no quantitative genetic differences in the aetiology of school achievement. Multivariate studies done to date have also shown that there is a substantial pleiotropy in school achievement in earlier school years, showing that achievement in the core subjects of English, mathematics and science is to a large extent influenced by the same genetic variants (Davis, Haworth, & Plomin, 2009b; Haworth, Meaburn, Harlaar, & Plomin, 2007; Kovas et al., 2007; Kovas & Plomin, 2007; Markowitz, Willemsen, Trumbetta, van Beijsterveldt, & Boomsma, 2005). Furthermore, research has shown that there is substantial genetic correlation between intelligence and academic achievement (Calvin et al., 2012; Deary, Johnson, & Houlihan, 2009; Deary, Strand, Smith, & Fernandes, 2007). This lead to the Generalist Genes Hypothesis that posits that to a large extent the same genes influence a range of cognitive abilities as well as academic achievement (Kovas & Plomin, 2006; Plomin & Kovas, 2005). However, the research had only considered achievement in English, mathematics and science in early school years. The work I did during my MSc year extended this showing that there is a substantial pleiotropy across the range of subjects children study at school, from English, mathematics and science, to humanities and art using both multivariate twin analyses and bivariate GREML-GCTA (genome-wide complex trait analyses - see methods) (Yang, Lee, Goddard, & Visscher, 2011, 2013). Furthermore, I showed that this pleiotropy was not explained by intelligence alone.

The work presented in this thesis extends this by examining a largely understudied area, second language achievement. We show why children differ so widely in second language learning and, using multivariate genetic analysis, we investigated the extent to which the heritability of second language learning is explained by first language achievement and intelligence.

Because educational achievement is so important to society and to children as individuals it is important to understand the causes and correlates of educational achievement. Research has shown that educational achievement is related to intelligence (Bartels et al., 2002; Deary et al., 2007; Petrill & Wilkerson, 2000; Tambs, Sundet, Magnus, & Berg, 1989), self-efficacy (Chamorro-Premuzic, Harlaar, Greven, & Plomin, 2010; Spinath, Spinath, Harlaar, & Plomin, 2006; Zimmerman, Bandura, & Martinez-Pons, 1992; Zuffianò et al., 2013), personality (Chamorro-Premuzic & Furnham, 2003; Conard, 2006; Laidra, Pullmann, & Allik, 2007), home and school environment (Davis-Kean, 2005; Son & Morrison, 2010), health, including childhood disorders (de Ridder et al., 2013; Fiscella & Kitzman, 2009; Pingault et al., 2011; Polderman, Boomsma, Bartels, Verhulst, & Huizink, 2010), and behavioural problems (Harold, Aitken, & Shelton, 2007; Johnson, McGue, & Iacono, 2006). However, all these predictors are correlated and few studies have considered these predictors together using a multivariate design. Furthermore, even fewer studies have been conducted using multivariate genetic designs to study the aetiology of covariation between various cognitive and non-cognitive predictors of school achievement.

The work presented in the current thesis extends the previous research by investigating how various cognitive and non-cognitive factors explain the individual differences in school achievement, and the extent to which all these heritable predictors explain the heritability of exam performance, considering both the independent and joint prediction of these factors while taking into account their inter-correlations.

One possible component of the non-cognitive portion of the heritability of educational achievement is personality. The research on the correlates of educational achievement in this thesis focuses on the relationship between academic achievement and personality to study the extent to which personality predicts and explains the heritability of school grades, and how well “Grit” (perseverance and passion for long-term goals as defined by Duckworth (Duckworth, Peterson, Matthews, & Kelly, 2007)) explains exam performance when controlling for other personality factors (Chapter 5). Even though Grit has been shown to be associated with school achievement and life success, most research has been done on restricted samples, such as university graduates, rather than considering the general population (Duckworth & Gross, 2014; Duckworth et al., 2007; Eskreis-Winkler, Shulman, Beal, & Duckworth, 2014). Little is known about why children differ in Grit and the aetiology of correlation between Grit and school achievement in a general population. Despite the lack of empirical evidence about the power of Grit to predict academic achievement beyond well-known personality traits, improving Grit has set as a target for intervention in the US Department of Education and the UK Department for Education. The work presented in the current thesis extends the research done to date considering the relationship between Grit and academic achievement, when controlling for the Big Five personality factors, using a UK representative twin sample.

The evidence from genetically sensitive studies done to date supports the movement from traditional education that is based on standardised one-size-fits-all curriculum, to more personalized education. Personalized education takes into account that children differ to a large extent because of genetic differences between them. Education is much more than what is imposed on children, as the effect of instruction depends on children's genetic propensities (Asbury & Plomin, 2013; Shakeshaft et al., 2013). This can be explained in terms of genotype-environment correlation where children select, modify and create their environments that are correlated with their genetic propensities (Asbury & Plomin, 2013). There are three types of gene-environmental correlations: passive, active and evocative. Passive gene-environment correlation occurs when children inherit both genes and environment from their parents, for example parents with genetic propensities leading to playing musical instruments would encourage their children to play musical instruments and would play musical instruments at home, so children are exposed to music from very early on. Active gene-environment correlation occurs when children seek out environments that are correlated with their genetic propensities, for example children with genetic propensities to read extensively would actively find books and visit libraries to read more. Evocative gene-environment correlation occurs when children evoke environmental reactions based on their genetic propensities, for example children with genetic propensities of high mathematical ability would be noticed by the teachers who would give them more challenging mathematical problems to solve (Asbury & Plomin, 2013; Knopik et al., 2017). Children make choices that are correlated with their genetic propensities, but little is known empirically about the aetiology of educational choices children make. The work presented in this thesis extends the previous research by studying educational achievement after compulsory education to investigate the aetiology of subject choice. At the end of compulsory education in the UK children can choose whether they want to continue their studies at A-level (General Certificate of Advanced Education), which is a prerequisite of university education. Around 50% of children in the UK continue to study at A-levels and they can for the first time choose the subjects they want to study. This allows for investigation of educational choice or appetite for learning and the aetiology of achievement in chosen subjects.

In summary, the research presented in this thesis aims to explore and explain the high heritability of educational attainment. It does so by seeking a) to explore whether heritability of educational attainment changes following a major social change, b) to establish the aetiology of second language learning and its association with first language learning and intelligence, c) to clarify why educational achievement is so highly heritable, d) to establish the extent to which educational achievement can be predicted from personality, and e) to elucidate the aetiology of aptitude and appetite for learning post compulsory education. A more detailed overview is presented below.

Methods

Sample

The research presented in the current thesis uses the twin design as well as DNA based methods, using data collected in the UK and in Estonia. This section gives a general overview of the samples and methods used, with more detailed information presented within the chapters concerned.

Estonian Genome Centre University of Tartu (EGCUT).

EGCUT is a population-based biobank that recruited 52,000 volunteers aged 18 and over. This makes up 5% of the adult population in Estonia. The study was set up to research complex human disease using national health records. DNA and plasma were collected through venous blood at first contact, DNA and plasma were immediately extracted from the blood and stored in EGCUT Core Laboratory in Tartu, Estonia. Genome-wide genotyping was assayed for 20 000 participants using three Illumina arrays: Illumina HumanCoreExome, Illumina Human370 CNV and Illumina OmniExpress. Phenotypic data collection included an extensive questionnaire about education, occupation, health and personality; anthropometric measures like height and weight were measured by research assistants in person at first contact (Leitsalu, Haller et al., 2015; Leitsalu, Alavere, Tammesoo, Leego, & Metspalu, 2015).

EGCUT has been shown to be reasonably representative of the Estonian population in terms of age, sex and geographical location, although females participate more actively than males, and younger people participate more actively than older people (detailed cohort description is available from Leitsalu et al. 2015) (Leitsalu, Haller, et al., 2015; Leitsalu, Alavere, et al., 2015).

The Twins Early Development Study (TEDS)

TEDS is a UK-representative twin study that recruited over 16,000 twin pairs born in England and Wales between 1994-1996. Although there has been some attrition, more than 10,000 twin pairs remain actively involved in the study. Rich cognitive and behavioural data have been collected from the twins over the two decades including their educational outcome measures. Importantly, TEDS was a representative sample at the first contact, and remains representative sample in terms of family SES and ethnicity (Haworth, Davis, & Plomin, 2013; Kovas et al., 2007; Oliver & Plomin, 2007). The work presented in this thesis used data collected at ages 16 and 18.

Measures

The studies in this thesis mainly used data collected in the Twins Early Development Study (TEDS; Chapters 3-6), with additional data collected in the Estonian Genome Centre, University of Tartu (EGCUT; Chapter 2). The exact measures are described in detail in the chapters concerned.
Data about the educational outcomes were collected from the TEDS twins through the questionnaires sent by mail or over telephone. Shortly after completing their GCSEs (General Certificate of the Secondary Education) or A-level exams (General Certificate of Education Advanced level), twins were contacted and asked to provide the results of their exams. These self-reported exam grades were shown to be reliable when verified using data obtained from the National Pupil Database (NPD) yielding a correlation of ~.99 (Chapters 3-6). Educational attainment and occupational status in Estonia were collected from participants when they attended the EGCUT research centre after the first contact (Chapter 2). All other data were collected in TEDS using online batteries, specifically created for data collection in TEDS and are described in detail in the chapters concerned.

Twin studies

Twins offer a powerful natural experiment to study the aetiology of traits of interest. Monozygotic (MZ) twins are genetically identical, while dizygotic (DZ) twins share on average 50% of their segregating genes, just like any other siblings; both pairs share their rearing environment when growing up in the same family. Capitalizing on the known genetic relatedness coefficients between MZ and DZ twins it is possible to estimate the genetic, shared environmental and non-shared environmental proportions of the variance. If MZ twins are more similar than DZ twins on a trait of interest then genetic influence on a trait is assumed. Environmental influences on a trait are everything else that is not attributable to genetics, and includes obvious environmental factors such as home and school environment, but also includes diet, disease phenotypes and prenatal hormone exposures. Environmental influences that contribute to similarity between twin pairs are classified as shared environmental influences, and environmental factors that do not contribute to similarities between twins form the non-shared environmental differences; importantly, this also includes the measurement error (Knopik et al., 2017). Heritability (A) can be roughly calculated by doubling the difference between MZ and DZ correlations using Falconer's formula, shared environmental influence (C) can be estimated by deducting the heritability estimate from the MZ correlations and non-shared environmental (E) factors can be calculated by deducting MZ correlations from unity (Rijsdijk & Sham, 2002). These ACE parameters can be calculated more accurately and with confidence intervals using structural equation models with maximum likelihood estimation.

Possible sex differences at the aetiological level can also be investigated by genetic sex limitation model fitting techniques (qualitative sex differences - the extent to which the same genes influence males and females; quantitative sex differences - the extent to which genes influence one gender more than the other) (Rijsdijk & Sham, 2002).

Bivariate genetic analysis extends univariate ACE analysis to the covariance between two traits. The ACE parameters can be estimated for the covariance between traits by comparing the cross-twin cross-trait correlations for MZ and DZ twin pairs. The extent to which these MZ correlations exceed DZ correlations indexes genetic mediation of the phenotypic correlation between the two traits. The contributions of C and E to the phenotypic correlation can also be estimated. Bivariate genetic analysis yields an additional statistic: the genetic correlation (r_G), which is an index of pleiotropy that indicates the extent to which the same genes influence two traits regardless of their heritabilities. The genetic correlation is independent of the heritabilities of two traits, in a sense that the heritability of both traits could be high, while the genetic correlation low and vice versa. Although this method of calculating the genetic correlation does not tell us anything about the underlying biological mechanisms, it does imply causality indicating that the same genetic variants influence both traits (Ligthart & Boomsma, 2012). Similarly, this method allows for an estimation of the shared environmental correlation (r_C) and the non-shared environmental correlation (r_E). Bivariate analyses can then be extended to multivariate analyses to study the aetiology covariation across multiple traits or the same trait longitudinally (Knopik et al., 2017; Rijsdijk & Sham, 2002). Specific models used in this thesis are explained in the chapters concerned (Chapters 3-6).

One of the most important and also most criticized assumptions of the classical twin design is the Equal Environments Assumption (EEA). EEA is an assumption that refers to the roughly equal shared environment for MZ twins and DZ twins. This assumption is crucial and is the basis of all twin studies and a vast amount of research done to date. If the assumptions of equal environment are not met, this could lead to a distortion of genetic and environmental effects. The main criticism against EEA is that MZ twins are treated more similarly and they tend to spend more time together, compared to DZ twins. There is some evidence suggesting that this is true and some MZ similarity is in fact explained by treatment effects from family, friends or teachers (Richardson & Norgate, 2005). Additionally, MZ twins share their prenatal environment due to a shared placenta, thus their prenatal environment is more similar compared to DZ twins. The impact of this could lead to an overestimation of genetic effects and an underestimation of environmental effects (Knopik et al., 2017; Rijsdijk & Sham, 2002). Conversely, MZ twins could be separated to encourage them to develop their individuality; for example, they could be separated into different classes at school, and this, in turn, could lead to underestimation of genetic effects. Additionally, the prenatal environment could be different for MZ compared to DZ twins. Arguably, there is more competition between MZ twins, especially if they share the same chorion. This is supported by the lower birth weight for MZ twins compared to DZ twins (and more often bigger birth weight differences), and could lead to an underestimation of genetic effects and an overestimation of environmental effects. Further research is needed to determine the effect of prenatal environment in relation to EEA (Knopik et al., 2017; Rijsdijk & Sham, 2002).

The EEA has been tested in various ways. One of the strategies to empirically test the EEA is to look at misclassified twins (twins who are perceived to be MZ twins when in fact they are DZ twins and vice versa) and comparing them to correctly classified twins. Misclassification seems to have very little or no effect and the EEA has been found to hold true (Conley, Rauscher, Dawes, Magnusson, & Siegal, 2013). Additionally, EEA can be tested if parents try to treat their twins differently intentionally, but twins do not show different phenotypic outcomes as compared to typical shared environment. EEA has been tested for several phenotypes using the designs described above: psychiatric illness (Kendler, Neale, Kessler, Heath, & Eaves, 1994); personality (Plomin, Willerman, & Loehlin, 1976); childhood experiences (Borkenau, Riemann, Angleitner, & Spinath, 2002); depression, anxiety and alcoholism (Hettema, Neale, & Kendler, 1995; Kendler, Neale, Kessler, Heath, & Eaves, 1992; Labuda, Svikis, & Pickens, 1997), cognitive ability and vocational interests (Loehlin & Nichols, 1976) and emotional and behavioural problems to name a few (Cronk et al., 2002). All these studies found little evidence for the violation of EEA.

Another important limitation of twin design involves assortative mating, in which mate selection is not done at random but is based on trait similarities. Assortative mating has been shown to be substantial on intelligence, especially on verbal ability (mate correlation of ~.40) (Knopik et al., 2017; Plomin & Deary, 2015; Vinkhuyzen, Van Der Sluis, Maes, & Posthuma, 2012). Assortative mating is also substantial for educational attainment, and there is now DNA evidence for genetic assortative mating, where a polygenic score created from a years of education genome-wide association (GWA) study (Okbay et al., 2016) significantly predicts partners' educational outcomes (Hugh-Jones, Verweij, St. Pourcain, & Abdellaoui, 2016). Assortative mating would increase DZ correlations relative to MZ correlations, and therefore could decrease the heritability estimates provided by the twin design (Knopik et al., 2017).

Additionally, the twin design estimates the relative proportion of variance or covariance that is explained by genetic, shared environmental and non-shared environmental proportions of variance or covariance in a particular population at a particular time. It gives population statistics and cannot tell anything about specific individuals or provide individual-specific prediction of outcomes.

Genome-wide Complex Trait Analyses (GCTA)

The Genome-wide Complex Trait Analysis (GCTA) software package allows us to study the proportion of phenotypic variance or covariance that is explained by all SNPs (single nucleotide polymorphisms) that are available on genotype arrays together, without testing the association of any single SNP individually (Lee, Yang, Goddard, Visscher, & Wray, 2012; Yang et al., 2010, 2011). This estimate is often called SNP heritability. This method does not use known genetic relatedness coefficients but estimates heritability from DNA only using unrelated individuals. SNP heritability is calculated using restricted maximum likelihood (REML) and the variance and covariance is decomposed using mixed linear models.

First, the genetic relatedness matrix (GRM) is calculated by weighting the pairwise genetic similarities with the allele frequencies across all SNPs on the DNA array. Individuals who are found to be even remotely related (equal or greater than fourth cousins) are removed from the analyses as it would otherwise bias the results (Trzaskowski et al., 2014; Yang et al., 2011, 2013). The matrix of pair-by-pair genetic similarity is compared to the matrix of pair-by-pair phenotypic similarity using the residual maximum likelihood estimation. The bivariate method extends the univariate model by comparing the pair-by-pair genetic similarity to the matrix of pair-by-pair phenotypic covariance matrix between two traits of interest (Lee et al., 2012).

GCTA, otherwise known as GREML, overcomes some of the limitations of the twin design. It does not rely on genetic relatedness of participants as it uses unrelated individuals. It also does not have the same assumptions, such as the EEA assumption. The major disadvantage of GCTA method is that very large samples are needed to reliably detect overall genetic similarity from the matrix of hundreds of thousands of SNPs genotyped on common SNP arrays. Additionally, the method captures only additive genetic effects of common SNPs. It is currently limited to the common SNPs used on SNP chips, whereas most DNA variation is rare. Also, GCTA does not capture gene-gene or gene-environment interplay (Yang et al., 2010), but these are unlikely to have a strong influence on any phenotype studied (Visscher, Hill, & Wray, 2008; Yang et al., 2010). Furthermore, as with the twin method, SNP heritability is a population estimate, not telling us anything about individual prediction. Notably, SNP heritability is usually half of what is shown using the twin method, because SNP heritability is limited to the additive effects of SNPs genotyped on the common DNA chips (Knopik et al., 2017); this is why the difference between SNP heritability and twin heritability is often referred to as the ‘missing heritability’ (Wray, Lee, Mehta, Vinkhuyzen, & Middeldorp, 2014). Nevertheless, GREML offers an additional quantitative genetic method to study the genetic architecture of complex phenotypes. An additional advantage of the method is that it offers a current ceiling for any GWA (genome-wide association) study attempting to identify specific SNPs associated with the trait of interest.

However, the GCTA package also makes certain assumptions; for example, it assumes that each SNP has the same effect on the phenotype. Furthermore, SNP heritability has been shown to vary according minor allelic frequency (MAF), genotype certainty, and linkage disequilibrium (LD) (Speed, Cai, Johnson, Nejentsev, & Balding, 2017; Speed, Hemani, Johnson, & Balding, 2012).

Just as with twin method, assortative mating could bias the estimates of SNP heritability. There is now molecular genetic evidence for substantial and significant assortative mating for educational attainment, in studies comparing the education associated loci between partners (Hugh-Jones et al., 2016; Robinson et al., 2017). The evidence for assortative mating, together with widespread pleiotropy, could have an effect on the genomic architecture of complex traits, and this could lead to inflation of SNP heritability for education of up to 20%, depending whether equilibrium has been reached in the population or not (Robinson et al., 2017).

Nevertheless, there is now ample evidence that almost every human trait is influenced by genetic factors (Polderman et al., 2015). This is supported by SNP based methods that have shown genetic influence for many traits including cognitive abilities (Deary et al., 2012; Marioni et al., 2014; Trzaskowski et al., 2014) and educational outcomes (G. Davies et al., 2016; N. M. Davies, Hemani, Timpson, Windmeijer, & Davey Smith, 2015; Krapohl & Plomin, 2016; Rietveld et al., 2013; Rimfeld et al., 2015).

Polygenic scores

There has been success in identifying specific genetic variants associated with complex traits using genome-wide association (GWA) studies, although progress has been slow. GWA studies aim to identify SNPs that are associated with complex traits in a general population, using linear regression between every SNP and a quantitative trait, or logistic regression testing the association between every SNP and binary trait including a diagnosis of cases vs. controls. Research to date has also shown that the number of discovered variants are correlated with the sample size, indicating that very large studies are needed to detect associations of very small independent effects; thus it is possible that current studies have led to many false negative results and there are still many loci that have not been identified because of the lack of power in GWA studies (Visscher, Brown, McCarthy, & Yang, 2012). GWA studies have shown that complex traits are incredibly polygenic, influenced by many genes of small effect (Visscher et al., 2012).

The genome-wide polygenic score (GPS) is a relatively new method that capitalizes on GWA studies to provide individual-specific prediction of genetic predisposition on a trait of interest (Chapter 2). Using the summary statistics of GWA 'discovery' samples, polygenic scores aggregate the effects of individual SNPs weighted by the strength of their association with the trait using p-values and effect sizes (β- weights) from the discovery sample to create polygenic scores for individuals in an independent 'target' sample. The GPS score is then associated with the trait of interest in the target sample to estimate the variance explained by GPS after accounting for covariates, such as age, sex, and population stratification. Importantly, GPS from a GWA analysis of a particular trait can be associated with other phenotypes, as twin- and SNP-based studies have shown substantial pleiotropy across a range of phenotypes (Dudbridge, 2013; Palla & Dudbridge, 2015; Wray, Lee, Mehta, Vinkhuyzen, & Middeldorp, 2014).

The advantage of GPS is that it provides an individual-specific prediction of genetic predisposition to complex traits, and can therefore shed light on understanding the biological mechanism of traits (Wray et al., 2014). Another major advantage of the GPS is that although extremely large samples are needed for GWA discovery, GPS does not need to be very large in the target sample. Furthermore, GPS, just as GCTA, is limited to estimating the additive genetic variance explained by common SNPs genotyped on the DNA chips. It is therefore, very informative to compare the GPS estimates to those of GCTA as SNP heritability provides the ceiling for GWA studies as well as for GPS prediction; the SNP heritability gives the upper limit of the individualised GPS prediction using the common SNPs on SNP chips (Selzam, Dale, et al., 2017). This is why the difference between SNP heritability and the heritability due to known variants is called 'the hidden heritability' (Wray et al., 2014). The power and accuracy of GPS is likely to increase considerably with more powerful GWA studies.

Summary of methods

The twin method is powerful in estimating the genetic variance and covariance of traits of interest even when specific genetic markers underlying the associations remain undiscovered. GCTA uses unrelated individuals and DNA markers (SNP heritability) to allow for an alternative method to study the genetic architecture of variance and covariance of complex traits. These two quantitative genetic methods, each with their advantages and limitations, provide converging evidence of genetic influence on complex traits such as educational achievement. The most powerful method to date offering individual prediction for school achievement is the GPS, which capitalizes on GWA discovery samples to estimate the genetic profiles of individuals (Krapohl et al., 2015; Selzam, Dale, et al., 2017; Selzam, Krapohl, et al., 2017). Multi-method approaches to study complex phenotypes offers the best hope for understanding the complex biological mechanisms underlying the individual variation in traits.

Overview

This thesis presents work done to further the understanding of aetiology and correlates of educational attainment. In the chapters following I aim to 1) investigate possible changes in genetic influence on educational attainment following major change in the environment; 2) investigate the extent to which educational achievement in second language learning is heritable and independent of genetic influence on first language achievement and intelligence; 3) establish the extent to which the high heritability of educational achievement is explained by a package of genetically influenced cognitive and non-cognitive traits; 4) clarify if personality predicts educational achievement; and 5) investigate the extent to which genetics affects appetite (subject choice for learning) as well as aptitude (exam performance) for learning.

While there is extensive literature showing that educational achievement is highly heritable, it is unclear how this high heritability might change with major environmental change. Chapter 2 explores the aetiology of educational attainment and occupational status in Estonia, comparing the heritability of these phenotypes during the Soviet era to those after Estonia regained independence in 1991. Previous evidence for the change of heritability in education is discussed, concluding that while there is some evidence for change in the aetiology of educational attainment across birth cohorts or following educational reform, there is no evidence of how heritability of educational attainment might change following an abrupt social change. Evidence is provided for increasing heritability after the collapse of the Soviet Union in Estonia. The chapter concludes with discussion and implications of the research, arguing that heritability of social outcomes is higher in a more meritocratic society; therefore the high heritability of educational attainment and occupational status could be considered as an index of equal opportunity in a society.

Educational achievement has been shown to be highly heritable across the subjects children study at school; however, most of the research has focused on achievement in English, mathematics and science and less is known about the aetiology and correlates of second language achievement. Chapter 3 reviews research on the heritability of educational achievement focusing on a largely under-studied area, second language achievement. We show that second language achievement is highly heritable across the various foreign languages children study at school. Using multivariate analyses we show that a third of the heritability of second language learning is explained by first language achievement (English grade), a further third is explained by intelligence, when controlling for first language achievement and a further third is unique genetic experience, not shared with first language learning and intelligence. The chapter ends with implications and further research suggestions.

Educational achievement is highly heritable, but it is unclear what psychological mechanisms contribute to this high heritability. Chapter 4 considers various cognitive and non-cognitive predictors to study the general landscape of heritability of school performance at the end of compulsory education (age 16). Using a genetic multivariate design, we assessed the joint as well as individual prediction of intelligence, self -efficacy, home and school environment, health, behavioural problems, personality and wellbeing on exam performance at age 16. The chapter concludes that heritability of educational achievement is explained by a package of genetically influenced traits. A case is made to highlight the importance of genetics in education highlighting the need for personalised learning that takes into account that children differ in part based on the genetic differences between them.

One of the non-cognitive correlates of educational achievement is personality. Chapter 5 focuses on personality as a predictor of school achievement, showing that personality, especially conscientiousness, is an important predictor of school achievement. This is the first study to assess the independent prediction of Grit (perseverance and passion for long-term goals) for school achievement using a large representative sample and a genetically sensitive design. We show that Grit adds little to the prediction of school achievement when the Big Five personality factors are controlled for. Furthermore, we show that Grit is essentially very similar to conscientiousness both phenotypically and genetically. We discuss the direct implications of the study to the policy decisions of education and propose future research directions.

At the end of compulsory education in the UK, children can choose whether they want to continue their studies at A-levels, a prerequisite for university entry, and around 50% choose to do so. Importantly, for the first time in their educational career they can freely choose the subjects they want to study. This facilitates research on the appetite for learning as well as aptitude (Chapter 6). We show that genetics plays an important part in explaining individual differences in appetite (subject choices) as well as aptitude of learning (exam grades of the chosen subjects). The results are discussed in terms of gene-environment correlation. A case is made supporting the personalised education that considers genetic influence on the appetite as well as aptitude for learning; given a choice children would choose and create their educational experiences partly based on their genetic propensities.

I conclude the thesis with a discussion about implications of the work and suggestions for future directions (Chapter 7).

References

Adler, N. E., Boyce, T., Chesney, M. A., Cohen, S., Folkman, S., Kahn, R. L., & Syme, S. L. (1994). Socioeconomic status and health: the challenge of the gradient. *American Psychologist*, *49*(1), 15–24. http://doi.org/http://dx.doi.org/10.1016/B0-08-043076-7/03827-4

Arendt, J. N. (2005). Does education cause better health? A panel data analysis using school reforms for identification. *Economics of Education Review*, *24*(2), 149–160. http://doi.org/10.1016/j.econedurev.2004.04.008

Asbury, K., & Plomin, R. (2013). *G is for Genes: The Impact of Genetics on Education and Achievement*. John Wiley & Sons.

Baker, L. A., Treloar, S. A., Reynolds, C. A., Heath, A. C., & Martin, N. G. (1996). Genetics of educational attainment in Australian twins: Sex differences and secular changes. *Behavior Genetics*, *26*(2), 89–102. http://doi.org/10.1007/BF02359887

Bartels, M., Rietveld, M. J. H., Van Baal, G. C. M., & Boomsma, D. I. (2002). Heritability of educational achievement in 12-year-olds and the overlap with cognitive ability. *Twin Research : The Official Journal of the International Society for Twin Studies*, *5*, 544–553. http://doi.org/10.1375/twin.5.6.544

Batty, G. D., Deary, I. J., & Gottfredson, L. S. (2007). Premorbid (early life) IQ and later mortality risk: Systematic review. *Annals of Epidemiology*, *17*(4), 278–288. http://doi.org/10.1016/j.annepidem.2006.07.010

Belsky, D. W., Moffitt, T. E., Corcoran, D. L., Domingue, B., Harrington, H., Hogan, S., … Caspi, A. (2016). The genetics of success: how single-nucleotide polymorphisms associated with educational attainment relate to life-course development. *Psychological Science*, *27*, 957–972. http://doi.org/10.1177/0956797616643070

Benjamin, D. J., Cesarini, D., van der Loos, M. J. H. M., Dawes, C. T., Koellinger, P. D., Magnusson, P. K. E., … Visscher, P. M. (2012). The genetic architecture of economic and political preferences. *Proceedings of the National Academy of Sciences*, *109*, 8026–8031. http://doi.org/10.1073/pnas.1120666109

Bloodsworth, J. (2016). *The myth of meritocracy*. London, UK: Biteback Publishing.

Borkenau, P., Riemann, R., Angleitner, A., & Spinath, F. M. (2002). Similarity of childhood experiences and personality resemblance in monozygotic and dizygotic twins: a test of the equal environments assumption. *Personality and Individual Differences*, *33*(2), 261–269. http://doi.org/10.1016/S0191-8869(01)00150-7

Boughton, J. (2012). *Tearing Down Walls: The International Monetary Fund, 1990-1999*. Washington, DC.

Branigan, A. R., Mccallum, K. J., & Freese, J. (2013). Variation in the heritability of educational attainment: An international meta-analysis. *Social Forces*, *92*(1), 109–140. http://doi.org/10.1093/sf/sot076

Calvin, C. M., Deary, I. J., Webbink, D., Smith, P., Fernandes, C., Lee, S. H., … Visscher, P. M. (2012). Multivariate genetic analyses of cognition and academic achievement from two population samples of 174,000 and 166,000 school children. *Behavior Genetics*, *42*(5), 699–710. http://doi.org/10.1007/s10519-012-9549-7

Carnaghan, E., & Bahry, D. (1990). Political Attitudes and the Gender Gap in the USSR. *Comparative Politics*, *22*(4), 379–399. http://doi.org/10.2307/421970

Chamorro-Premuzic, T., & Furnham, A. (2003). Personality predicts academic performance: Evidence from two longitudinal university samples. *Journal of Research in Personality*. http://doi.org/10.1016/S0092-6566(02)00578-0

Chamorro-Premuzic, T., Harlaar, N., Greven, C. U., & Plomin, R. (2010). More than just IQ: A longitudinal examination of self-perceived abilities as predictors of academic performance in a large sample of UK twins. *Intelligence*, *38*, 385–392. http://doi.org/10.1016/j.intell.2010.05.002

Colodro-Conde, L., Rijsdijk, F., Tornero-Gómez, M. J., Sánchez-Romera, J. F., & Ordoñana, J. R. (2015). Equality in educational policy and the heritability of educational attainment. *PLoS ONE*, *10*(11), e0143796. http://doi.org/10.1371/journal.pone.0143796

Conard, M. A. (2006). Aptitude is not enough: How personality and behavior predict academic performance. *Journal of Research in Personality*, *40*, 339–346. http://doi.org/10.1016/j.jrp.2004.10.003

Conley, D., Rauscher, E., Dawes, C., Magnusson, P. K. E., & Siegal, M. L. (2013). Heritability and the equal environments assumption: evidence from multiple samples of misclassified twins. *Behavior Genetics*, *43*(5), 415–26. http://doi.org/10.1007/s10519-013-9602-1

Coventry, W., Antón-Méndez, I., Ellis, E. M., Levisen, C., Byrne, B., van Daal, V. H. P., & Ellis, N. C. (2012). The etiology of individual differences in second language acquisition in Australian school students: A behavior-genetic study. *Language Learning*, *62*, 880–901. http://doi.org/10.1111/j.1467-9922.2012.00718.x

Cronk, N. J., Slutske, W. S., Madden, P. a F., Bucholz, K. K., Reich, W., & Heath, A. C. (2002). Emotional and behavioral problems among female twins: an evaluation of the equal environments assumption. *Journal of the American Academy of Child and Adolescent Psychiatry*, *41*(7), 829–37. http://doi.org/10.1097/00004583-200207000-00016

Cutler, D. M., & Lleras-Muney, A. (2012). *Education and health: insights from international comparisons* (No. 17738). *NBER Working Papers*.

Cutler, D. M., Lleras-Muney, A., & Vogl, T. (2008). *Socioeconomic status and health: dimensions and mechanisms* (No. 14333). *NBER Working Papers*.

Davies, G., Marioni, R. E., Liewald, D. C., Hill, W. D., Hagenaars, S. P., Harris, S. E., … Deary, I. J. (2016). Genome-wide association study of cognitive functions and educational attainment in UK Biobank (N=112 151). *Molecular Psychiatry*, *21*(6), 758–67. http://doi.org/10.1038/mp.2016.45

Davies, N. M., Hemani, G., Timpson, N. J., Windmeijer, F., & Davey Smith, G. (2015). The role of common genetic variation in educational attainment and income: evidence from the National Child Development Study. *Scientific Reports*, *5*(October), 16509. http://doi.org/10.1038/srep16509

Davis-Kean, P. E. (2005). The influence of parent education and family income on child achievement: the indirect role of parental expectations and the home environment. *Journal of Family Psychology : JFP : Journal of the Division of Family Psychology of the American Psychological Association (Division 43)*, *19*(2), 294–304. http://doi.org/10.1037/0893-3200.19.2.294

Davis, O. S. P., Band, G., Pirinen, M., Haworth, C. M. A., Meaburn, E. L., Kovas, Y., … Spencer, C. C. a. (2014). The correlation between reading and mathematics ability at age twelve has a substantial genetic component. *Nature Communications*, *5*. http://doi.org/10.1038/ncomms5204

Davis, O. S. P., Haworth, C. M. A., & Plomin, R. (2009a). Learning abilities and disabilities: generalist genes in early adolescence. *Cognitive Neuropsychiatry*, *14*(4–5), 312–31. http://doi.org/10.1080/13546800902797106

Davis, O. S. P., Haworth, C. M. A., & Plomin, R. (2009b). Learning abilities and disabilities: generalist genes in early adolescence. *Cognitive Neuropsychiatry*, *14*, 312–331.

http://doi.org/10.1080/13546800902797106

de Ridder, K. A. A., Pape, K., Johnsen, R., Holmen, T. L., Westin, S., & Bjorngaard, J. H. (2013). Adolescent Health and High School Dropout: A Prospective Cohort Study of 9000 Norwegian Adolescents (The Young-HUNT). *PLoS ONE*, *8*(9). http://doi.org/10.1371/journal.pone.0074954

Deary, I. J., Johnson, W., & Houlihan, L. M. (2009). Genetic foundations of human intelligence. *Human Genetics*, *126*, 215–232. http://doi.org/10.1007/s00439-009-0655-4

Deary, I. J., Strand, S., Smith, P., & Fernandes, C. (2007). Intelligence and educational achievement. *Intelligence*, *35*(1), 13–21. http://doi.org/10.1016/j.intell.2006.02.001

Deary, I. J., Yang, J., Davies, G., Harris, S. E., Tenesa, A., Liewald, D., … Visscher, P. M. (2012). Genetic contributions to stability and change in intelligence from childhood to old age. *Nature*. http://doi.org/10.1038/nature10781

Delaneau, O., Zagury, J.-F., & Marchini, J. (2013). Improved whole-chromosome phasing for disease and population genetic studies. *Nature Methods*, *10*(1), 5–6. http://doi.org/10.1038/nmeth.2307

Domingue, B. W., Belsky, D. W., Conley, D., Harris, K. M., & Boardman, J. D. (2015). Polygenic influence on educational attainment. *AERA Open*, *1*(3), 2332858415599972. http://doi.org/10.1177/2332858415599972

Duckworth, A. L., & Gross, J. J. (2014). Self-Control and Grit: related but separable reterminants of success. *Current Directions in Psychological Science*, *23*(5), 319–325. http://doi.org/10.1177/0963721414541462

Duckworth, A. L., Peterson, C., Matthews, M. D., & Kelly, D. R. (2007). Grit: perseverance and passion for long-term goals. *Journal of Personality and Social Psychology*, *92*(6), 1087–101. http://doi.org/10.1037/0022-3514.92.6.1087

Dudbridge, F. (2013). Power and predictive accuracy of polygenic risk scores. *PLoS Genetics*, *9*(3), e1003348. http://doi.org/10.1371/journal.pgen.1003348

Eskreis-Winkler, L., Shulman, E. P., Beal, S. A., & Duckworth, A. L. (2014). The grit effect: Predicting retention in the military, the workplace, school and marriage. *Frontiers in Psychology*, *5*. http://doi.org/10.3389/fpsyg.2014.00036

Euesden, J., Lewis, C. M., & O'Reilly, P. F. (2014). PRSice: Polygenic Risk Score software. *Bioinformatics*, *31*(9), 1466–1468. http://doi.org/10.1093/bioinformatics/btu848

Fiscella, K., & Kitzman, H. (2009). Disparities in academic achievement and health: the intersection of child education and health policy. *Pediatrics*, *123*(3), 1073–80. http://doi.org/10.1542/peds.2008-0533

Fisher, R. . (1921). On the probable error of a coefficient of correlation deduced from a small sample. *Metron*, *1*, 3–32.

Furnham, A., & Cheng, H. (2016). Childhood cognitive ability predicts adult financial well-being. *Journal of Intelligence*, *5*(1), 3. http://doi.org/10.3390/jintelligence5010003

Ganzeboom, H. B. G. (2010). A New International Socio-Economic Index [ISEI] of occupational status for the International Standard Classification of Occupation 2008 [ISCO-08] constructed with data from the ISSP 2002-2007; with an analysis of quality of occupational measurement in ISS. *Annual Conference of International Sociall Survey Programme , Lisbon.*

Ganzeboom, H. B., & Treiman, D. J. (2003). Three internationally standardised measures for comparative research on occupational status. In J. H. P. Hoffmeyer-Zlotnik & Christof Wolf (Eds.), *Advances in Cross-National Comparison. A European Working Book for Demographic and Socio-Economic Variables.* (pp. 159–193). New York: Kluwer Academic Press.

Gottfredson, L. S. (1997). Why g matters: The complexity of everyday life. *Intelligence*. http://doi.org/10.1016/S0160-2896(97)90014-3

Hanscombe, K. B., Trzaskowski, M., Haworth, C. M. A., Davis, O. S. P., Dale, P. S., & Plomin, R. (2012). Socioeconomic status (SES) and children's intelligence (IQ): in a UK-representative sample SES moderates the environmental, not genetic, effect on IQ. *PloS One*, *7*(2), e30320. http://doi.org/10.1371/journal.pone.0030320

Harold, G. T., Aitken, J. J., & Shelton, K. H. (2007). Inter-parental conflict and children's academic attainment: a longitudinal analysis. *Journal of Child Psychology and Psychiatry, and Allied Disciplines*, *48*(12), 1223–32. http://doi.org/10.1111/j.1469-7610.2007.01793.x

Hart, S. A., Petrill, S. A., Thompson, L. A., & Plomin, R. (2009). The ABCs of math: A genetic analysis of mathematics and its links with reading ability and general cognitive ability. *Journal of Educational Psychology*. http://doi.org/10.1037/a0015115

Haworth, C. M. A., Davis, O. S. P., & Plomin, R. (2013). Twins Early Development Study (TEDS): A genetically sensitive investigation of cognitive and behavioral development from childhood to young adulthood. *Twin Research and Human Genetics : The Official Journal of the International Society for Twin Studies*, *16*(1), 117–25. http://doi.org/10.1017/thg.2012.91

Haworth, C. M. A., Meaburn, E. L., Harlaar, N., & Plomin, R. (2007). Reading and Generalist Genes. *Mind, Brain and Education : The Official Journal of the International Mind, Brain, and Education Society*, *1*(4), 173–180. http://doi.org/10.1111/j.1751-228X.2007.00018.x

Heath, A. C., Berg, K., Eaves, L. J., Solaas, M. H., Corey, L. A., Sundet, J., … Nance, W. E. (1985). Education policy and the heritability of educational attainment. *Nature*. http://doi.org/10.1038/314734a0

Hettema, J. M., Neale, M. C., & Kendler, K. S. (1995). Physical similarity and the equal-environment assumption in twin studies of psychiatric disorders. *Behavior Genetics*, *25*, 327–335. http://doi.org/10.1007/BF02197281

Hill, W. D., Hagenaars, S. P., Marioni, R. E., Harris, S. E., Liewald, D. C., Davies, G., … Deary, I. J. (2016). Molecular genetic contributions to social deprivation and household income in UK Biobank (n = 112,151). *Current Biology*, *26*(22), 3083–3089. http://doi.org/10.1101/043000

Hollingshead, A. (1975). Four factor index of social status. *Yale Journal of Sociology*.

Howie, B. N., Donnelly, P., & Marchini, J. (2009). A flexible and accurate genotype imputation method for the next generation of genome-wide association studies. *PLoS Genetics*, *5*(6), e1000529. http://doi.org/10.1371/journal.pgen.1000529

Hugh-Jones, D., Verweij, K. J. H., St. Pourcain, B., & Abdellaoui, A. (2016). Assortative mating on educational attainment leads to genetic spousal resemblance for polygenic scores. *Intelligence*, *59*, 103–108. http://doi.org/10.1016/j.intell.2016.08.005

Hyytinen, A., Ilmakunnas, P., Johansson, E., & Toivanen, O. (2013). *Heritability of lifetime income* (No. 364). *Helsinki Centre of Economic Research*.

Johnson, W., McGue, M., & Iacono, W. G. (2006). Genetic and environmental influences on academic achievement trajectories during adolescence. *Developmental Psychology*, *42*(3), 514–32. http://doi.org/10.1037/0012-1649.42.3.514

Katz, K. (2001). *Gender, work and wages in the Soviet Union: a legacy of discrimination*. Palgrave Macmillan, UK.

Kendler, K. S., Neale, M. C., Kessler, R. C., Heath, A. C., & Eaves, L. J. (1992). Major depression and generalized anxiety disorder. Same genes, (partly) different environments? *Archives of General Psychiatry*, *49*, 716–722. http://doi.org/10.1001/archpsyc.1992.01820090044008

Kendler, K. S., Neale, M. C., Kessler, R. C., Heath, A. C., & Eaves, L. J. (1994). Parental treatment and the equal environment assumption in twin studies of psychiatric illness. *Psychological Medicine*, *24*(3), 579–590. http://doi.org/10.1017/S0033291700027732

Knopik, V. S., Neiderhiser, J. M., DeFries, J. C., & Plomin, R. (2017). *Behavioral Genetics. 7th ed*. Worth Publishers, New York.

Kong, A., Frigge, M. L., Thorleifsson, G., Stefansson, H., Young, A. I., Zink, F., … Stefansson, K. (2017). Selection against variants in the genome associated with educational attainment. *Proceedings of the National Academy of Sciences*, *114*(5), E727-32. http://doi.org/10.1073/pnas.1612113114

Kovas, Y., Haworth, C. M. A., Dale, P. S., & Plomin, R. (2007). The genetic and environmental origins of learning abilities and disabilities in the early school years. *Monographs of the Society for Research in Child Development*, *72*(3), 1–144. http://doi.org/10.1111/j.1540-5834.2007.00439.x

Kovas, Y., & Plomin, R. (2006). Generalist genes: implications for the cognitive sciences. *Trends in Cognitive Sciences*, *10*, 198–203. http://doi.org/10.1016/j.tics.2006.03.001

Kovas, Y., & Plomin, R. (2007). Learning abilities and disabilities: Generalist genes, specialist environments. *Current Directions in Psychological Science*, *16*, 284–288. http://doi.org/10.1111/j.1467-8721.2007.00521.x

Kovas, Y., Voronin, I., Kaydalov, A., Malykh, S. B., Dale, P. S., & Plomin, R. (2013). Literacy and numeracy are more heritable than intelligence in primary school. *Psychological Science*, *24*, 2048–56. http://doi.org/10.1177/0956797613486982

Krapohl, E., Euesden, J., Zabaneh, D., Pingault, J., Rimfeld, K., Stumm, S. Von, … Plomin, R. (2015). Phenome-wide analysis of genome-wide polygenic scores. *Molecular Psychiatry*, (21), 1188–1193. http://doi.org/10.1038/mp.2015.126

Krapohl, E., & Plomin, R. (2016). Genetic link between family socioeconomic status and children's educational achievement estimated from genome-wide SNPs. *Molecular Psychiatry*, *21*, 437–443. http://doi.org/10.1038/mp.2015.2

Krapohl, E., Rimfeld, K., Shakeshaft, N. G., Trzaskowski, M., McMillan, A., Pingault, J.-B., … Plomin, R. (2014). The high heritability of educational achievement reflects many genetically influenced traits, not just intelligence. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(42), 15273–15278. http://doi.org/10.1073/pnas.1408777111

Kromhout, H. (2003). The use of occupation and industry classifications in general population studies. *International Journal of Epidemiology*, *32*(3), 419–428. http://doi.org/10.1093/ije/dyg080

Laar, M. (2007a). *Estonia's way*. Tallinn, Estonia: Pegasus, Tallinn, Estonia.

Laar, M. (2007b). The Estonian economic miracle. *Backgrounder*, *2060*, 1–12.

Labuda, M. C., Svikis, D. S., & Pickens, R. W. (1997). Twin closeness and co-twin risk for substance use disorders : assessing the impact of the equal environment assumption. *Psychiatry Research*, *70 (3)*, 155–164. http://doi.org/10.1016/S0165-1781(97)03045-X

Laidra, K., Pullmann, H., & Allik, J. (2007). Personality and intelligence as predictors of academic achievement: A cross-sectional study from elementary to secondary school. *Personality and Individual Differences*, *42*(3), 441–451. http://doi.org/10.1016/j.paid.2006.08.001

Lee, S. H., Yang, J., Goddard, M. E., Visscher, P. M., & Wray, N. R. (2012). Estimation of pleiotropy between complex diseases using single-nucleotide polymorphism-derived genomic relationships and restricted maximum likelihood. *Bioinformatics*, *28*, 2540–2542. http://doi.org/10.1093/bioinformatics/bts474

Lehmann, E. (1975). *Nonparametric Statistical Methods Based on Ranks*. Holden-Day, San Francisco, CA.

Leitsalu, L., Alavere, H., Tammesoo, M.-L., Leego, E., & Metspalu, A. (2015). Linking a Population Biobank with National Health Registries—The Estonian Experience. *Journal of Personalized Medicine*, *5*(2), 96–106. http://doi.org/10.3390/jpm5020096

Leitsalu, L., Haller, T., Esko, T., Tammesoo, M. L., Alavere, H., Snieder, H., … Metspalu, A. (2015). Cohort profile: Estonian Biobank of the Estonian Genome Center, University of Tartu. *International Journal of Epidemiology*, *44*(4), 1137–1147. http://doi.org/10.1093/ije/dyt268

Lichtenstein, P., Pedersen, N. L., & McClearn, G. E. (1992). The Origins of Individual Differences in Occupational Status and Educational Level: A Study of Twins Reared Apart and Together. *Acta Sociologica*, *35*(1), 13–31. http://doi.org/10.1177/000169939203500102

Ligthart, L., & Boomsma, D. I. (2012). Causes of Comorbidity: Pleiotropy or Causality? Shared Genetic and Environmental Influences on Migraine and Neuroticism. *Twin Research and Human Genetics*, *15*(2), 158–165. http://doi.org/10.1375/twin.15.2.158

Loehlin, J. C., & Nichols, R. C. (1976). *Heredity, Environment, & Personality: A Study of 850 Sets of Twins*. University of Texas Press.

Lykken, D. T., Bouchard Jr., T. J., McGue, M., & Tellegen, A. (1990). The Minnesota Twin Family Registry: some initial findings. *Acta Genet Med Gemellol*, *39*(1), 35–70.

http://doi.org/10.1017/S0001566000005572

Marioni, R. E., Davies, G., Hayward, C., Liewald, D., Kerr, S. M., Campbell, A., … Deary, I. J. (2014). Molecular genetic contributions to socioeconomic status and intelligence. *Intelligence*, *44*, 26–32. http://doi.org/10.1016/j.intell.2014.02.006

Markowitz, E. M., Willemsen, G., Trumbetta, S. L., van Beijsterveldt, T. C. E. M., & Boomsma, D. I. (2005). The etiology of mathematical and reading (dis)ability covariation in a sample of Dutch twins. *Twin Research and Human Genetics : The Official Journal of the International Society for Twin Studies*, *8*, 585–593. http://doi.org/10.1375/twin.8.6.585

OECD. (2011). *Equity and Quality in Education - Supporting Disadvantaged Students and Schools*.

OECD. (2016). *Education Policy Outlook: Estonia*.

Okbay, A., Beauchamp, J. P., Fontana, M., Lee, J. J., Pers, T. ., Rietveld, C. A., … Pickrell, J. K. (2016). Genome-wide association study identifies 74 loci associated with educational attainment. *Nature*, *533*(7604), 539–542. http://doi.org/10.1038/nature17671

Oliver, B. R., & Plomin, R. (2007). Twins' Early Development Study (TEDS): a multivariate, longitudinal genetic investigation of language, cognition and behavior problems from childhood through adolescence. *Twin Research and Human Genetics : The Official Journal of the International Society for Twin Studies*, *10*, 96–105. http://doi.org/10.1375/twin.5.5.444

Oreopoulos, P., & Salvanes, K. G. (2011). Priceless: The nonpecuniary benefits of schooling. *Journal of Economic Perspectives*, *25*(1), 159–184. http://doi.org/10.1257/jep.25.1.159

Organisation for Economic Co-operation and Development (OECD). (2013). *Education at a Glance 2013: Highlights. Oecd*.

Palla, L., & Dudbridge, F. (2015). A fast method that uses polygenic scores to estimate the variance explained by genome-wide marker panels and the proportion of variants affecting a trait. *American Journal of Human Genetics*, *97*(2), 250–259. http://doi.org/10.1016/j.ajhg.2015.06.005

Petrill, S. A., Deater-Deckard, K., Thompson, L. A., Dethorne, L. S., & Schatschneider, C. (2006). Reading skills in early readers: genetic and shared environmental influences. *Journal of Learning Disabilities*, *39*(1), 48–55. http://doi.org/10.1177/00222194060390010501

Petrill, S. A., Hart, S. A., Harlaar, N., Logan, J., Justice, L. M., Schatschneider, C., … Cutting, L. (2010). Genetic and environmental influences on the growth of early reading skills. *Journal of Child Psychology and Psychiatry and Allied Disciplines*, *51*, 660–667. http://doi.org/10.1111/j.1469-7610.2009.02204.x

Petrill, S. A., & Wilkerson, B. (2000). Intelligence and achievement: A behavioral genetic perspective. *Educational Psychology Review*, *12*(2), 185–199. http://doi.org/10.1023/A:1009023415516

Piketty, T. (2014). *Capital in the twenty-first century*. Harvard, US: Harvard University Press.

Pingault, J. B., Tremblay, R. E., Vitaro, F., Carbonneau, R., Genolini, C., Falissard, B., & Cote, S. M. (2011). Childhood trajectories of inattention and hyperactivity and prediction of educational attainment in early adulthood: A 16-year longitudinal population-based study. *American Journal of Psychiatry*, *168*(11), 1164–1170. http://doi.org/10.1176/appi.ajp.2011.10121732

Plomin, R., & Deary, I. J. (2015). Genetics and intelligence differences: five special findings. *Molecular Psychiatry*, 20(1), 98–108. http://doi.org/10.1038/mp.2014.105

Plomin, R., & Kovas, Y. (2005). Generalist genes and learning disabilities. *Psychological Bulletin*, *131*(4), 592–617. http://doi.org/10.1037/0033-2909.131.4.592

Plomin, R., Willerman, L., & Loehlin, J. C. (1976). Resemblance in appearance and the equal environments assumption in twin studies of personality traits. *Behavior Genetics*, *6*(1), 43–52.

Polderman, T. J. C., Benyamin, B., de Leeuw, C. A., Sullivan, P. F., van Bochoven, A., Visscher, P. M., & Posthuma, D. (2015). Meta-analysis of the heritability of human traits based on fifty years of twin studies. *Nature Genetics*, *47*(7), 702–709. http://doi.org/10.1038/ng.3285

Polderman, T. J. C., Boomsma, D. I., Bartels, M., Verhulst, F. C., & Huizink, A. C. (2010). A systematic review of prospective studies on attention problems and academic achievement. *Acta Psychiatrica Scandinavica*, *122*, 271–284. http://doi.org/10.1111/j.1600-0447.2010.01568.x

Purcell, S., Neale, B., Todd-Brown, K., Thomas, L., Ferreira, M. A. R., Bender, D., … Sham, P. C. (2007). PLINK: A tool set for whole-genome association and population-based linkage analyses. *American Journal of Human Genetics*, *81*(3), 559–575. http://doi.org/10.1086/519795

Richardson, K., & Norgate, S. (2005). The equal environments assumption of classical twin studies may not hold. *British Journal of Educational …*, *75*, 339–350. http://doi.org/10.1348/000709904X24690

Rietveld, C. A., Medland, S. E., Derringer, J., Yang, J., Esko, T., Martin, N. W., … Koellinger, P. D. (2013). GWAS of 126,559 individuals identifies genetic variants associated with educational attainment. *Science*, *340*(6139), 1467–71. http://doi.org/10.1126/science.1235488

Rijsdijk, F. V, & Sham, P. C. (2002). Analytic approaches to twin data using structural equation models. *Briefings in Bioinformatics*, *3*(2), 119–133. http://doi.org/10.1093/bib/3.2.119

Rimfeld, K., Ayorech, Z., Dale, P. S., Kovas, Y., & Plomin, R. (2016). Genetics affects choice of academic subjects as well as achievement. *Scientific Reports*, *6*, 26373. http://doi.org/10.1038/srep26373

Rimfeld, K., Kovas, Y., Dale, P. S., & Plomin, R. (2015). Pleiotropy across academic subjects at the end of compulsory education. *Scientific Reports*, *5*, 11713. http://doi.org/10.1038/srep11713

Robinson, M. R., Kleinman, A., Graff, M., Vinkhuyzen, A. A. E., Couper, D., Miller, M. B., … Visscher, P. M. (2017). Genetic evidence of assortative mating in humans. *Nature Human Behaviour*, *1*(1), 16. http://doi.org/10.1038/s41562-016-0016

Saar, E. (1997). Transitions to Tertiary Education in Belarus and the Baltic Countries. *European Sociological Review*, *13*(2), 139–158. http://doi.org/https://doi.org/10.1093/oxfordjournals.esr.a018209

Saar, E. (2010). Changes in intergenerational mobility and educational inequality in Estonia: Comparative analysis of cohorts born between 1930 and 1974. *European Sociological Review*, *26*(3), 367–383. http://doi.org/10.1093/esr/jcp049

Samuelsson, S., Byrne, B., Quain, P., Wadsworth, S., Corley, R., DeFries, J. C., … Olson, R. (2005).

Environmental and genetic influences on prereading skills in Australia, Scandinavia, and the United States. *Journal of Educational Psychology*. http://doi.org/10.1037/0022-0663.97.4.705

Selzam, S., Dale, P. S., Wagner, R. K., DeFries, J. C., Cederlöf, M., O'Reilly, P. F., … Plomin, R. (2017). Genome-wide polygenic scores predict reading performance throughout the school years. *Scientific Studies of Reading*, 1–16. http://doi.org/10.1080/10888438.2017.1299152

Selzam, S., Krapohl, E., von Stumm, S., O'Reilly, P. F., Rimfeld, K., Kovas, Y., … Plomin, R. (2017). Predicting educational achievement from DNA. *Molecular Psychiatry*, *22*, 267–272. http://doi.org/10.1038/mp.2016.107

Shakeshaft, N. G., Trzaskowski, M., McMillan, A., Rimfeld, K., Krapohl, E., Haworth, C. M. A., … Plomin, R. (2013). Strong genetic influence on a UK nationwide test of educational achievement at the end of compulsory education at age 16. *PLoS ONE*, *8*, e80341. http://doi.org/10.1371/journal.pone.0080341

Silova, I., & Magno, C. (2004). Gender equity unmasked: democracy, gender, and education in Central/Southeastern Europe and the former Soviet Union. *Comparative Education Review*, *48*(4), 417–442. http://doi.org/10.1086/423358

Sirin, S. R. (2005). Socioeconomic Status and Academic Achievement: A Meta-Analytic Review of Research. *Review of Educational Research*, *75*(3), 417–453. http://doi.org/10.3102/00346543075003417

Son, S.-H., & Morrison, F. J. (2010). The nature and impact of changes in home learning environment on development of language and academic skills in preschool children. *Developmental Psychology*, *46*(5), 1103–18. http://doi.org/10.1037/a0020065

Speed, D., Cai, N., Johnson, M., Nejentsev, S., & Balding, D. (2017). Re-evaluation of SNP heritability in complex human traits. *Nature Genetics*, *49*, 986–992. http://doi.org/10.1038/ng.3865

Speed, D., Hemani, G., Johnson, M. R., & Balding, D. J. (2012). Improved heritability estimation from genome-wide SNPs. *American Journal of Human Genetics*, *91*, 1011–1021. http://doi.org/10.1016/j.ajhg.2012.10.010

Spinath, B., Spinath, F. M., Harlaar, N., & Plomin, R. (2006). Predicting school achievement from general cognitive ability, self-perceived ability, and intrinsic value. *Intelligence*, *34*(4), 363–374. http://doi.org/10.1016/j.intell.2005.11.004

Tambs, K., Sundet, J. M., Magnus, P., & Berg, K. (1989). Genetic and environmental contributions to the covariance between occupational status, educational attainment, and IQ: A study of twins. *Behavior Genetics*, *19*(2), 209–222. http://doi.org/10.1007/BF01065905

Titma, M., & Roots, A. (2006). Intragenerational Mobility in Successor States of the USSR. *European Societies*, *8*(4), 493–526. http://doi.org/10.1080/14616690500342618

Titma, M., Tuma, N. B., & Roosma, K. (2003). Education as a Factor in Intergenerational Mobility in Soviet Society. *European Sociological Review*. http://doi.org/10.1093/esr/19.3.281

Trzaskowski, M., Harlaar, N., Arden, R., Krapohl, E., Rimfeld, K., McMillan, A., … Plomin, R.

(2014). Genetic influence on family socioeconomic status and children's intelligence. *Intelligence*, *42*(100), 83–88. http://doi.org/10.1016/j.intell.2013.11.002

Van Der Waerden BL. (1975). On the sources of my book Moderne Algebra. *Historia Mathematica*, *2*(1), 31–40.

Vinkhuyzen, A. A. E., Van Der Sluis, S., Maes, H. H. M., & Posthuma, D. (2012). Reconsidering the heritability of intelligence in adulthood: Taking assortative mating and cultural transmission into account. *Behavior Genetics*, *42*(2), 187–198. http://doi.org/10.1007/s10519-011-9507-9

Visscher, P. M., Brown, M. A., McCarthy, M. I., & Yang, J. (2012). Five years of GWAS discovery. *American Journal of Human Genetics*. http://doi.org/10.1016/j.ajhg.2011.11.029

Visscher, P. M., Hemani, G., Vinkhuyzen, A. A. E., Chen, G. B., Lee, S. H., Wray, N. R., … Yang, J. (2014). Statistical Power to Detect Genetic (Co)Variance of Complex Traits Using SNP Data in Unrelated Samples. *PLoS Genetics*, *10*(4), e1004269. http://doi.org/10.1371/journal.pgen.1004269

Visscher, P. M., Hill, W. G., & Wray, N. R. (2008). Heritability in the genomics era — concepts and misconceptions. *Nature Reviews Genetics*, *9*(4), 255–266. http://doi.org/10.1038/nrg2322

von Stumm, S., Deary, I. J., & Hagger-Johnson, G. (2013). Life-course pathways to psychological distress: a cohort study. *BMJ Open*, *3*(5), e002772. http://doi.org/10.1136/bmjopen-2013-002772

Wadsworth, S. J., DeFries, J. C., Fulker, D. W., & Plomin, R. (1995). Cognitive ability and academic achievement in the Colorado adoption project: A multivariate genetic analysis of parent-offspring and sibling data. *Behavior Genetics*, *25*, 1–15. http://doi.org/10.1007/BF02197237

Wainwright, M. a, Wright, M. J., Geffen, G. M., Luciano, M., & Martin, N. G. (2005). The genetic basis of academic achievement on the Queensland Core Skills Test and its shared genetic variance with IQ. *Behavior Genetics*, *35*(2), 133–45. http://doi.org/10.1007/s10519-004-1014-9

White, K. R. (1982). The Relation Between Socioeconomic Status and Academic Achievement. *Psychological Bulletin*, *91*(3), 461–481. http://doi.org/10.1037/0033-2909.91.3.461

Wolf, C. (1997). The ISCO-88 International Standard Classification Of Occupations in cross-national survey research. *Bulletin de Methodologie Sociologique*, *54*(1), 23–40.

Wray, N. R., Lee, S. H., Mehta, D., Vinkhuyzen, A. A. E., & Middeldorp, C. M. (2014). Research Review : Polygenic methods and their application to psychiatric traits. *The Journal of Child Psychology and Psychiatry*, *55*(10), 1068–1087. http://doi.org/10.1111/jcpp.12295

Yang, J., Benyamin, B., McEvoy, B. P., Gordon, S., Henders, A. K., Nyholt, D. R., … Visscher, P. M. (2010). Common SNPs explain a large proportion of the heritability for human height. *Nature Genetics*, *42*(7), 565–9. http://doi.org/10.1038/ng.608

Yang, J., Lee, S. H., Goddard, M. E., & Visscher, P. M. (2011). GCTA: a tool for genome-wide complex trait analysis. *American Journal of Human Genetics*, *88*, 76–82. http://doi.org/10.1016/j.ajhg.2010.11.011

Yang, J., Lee, S. H., Goddard, M. E., & Visscher, P. M. (2013). Genome-wide complex trait analysis (GCTA): Methods, data analyses, and interpretations. *Methods in Molecular Biology*, *1019*, 215–

236. http://doi.org/10.1007/978-1-62703-447-0-9

Young, M. (1965). *The rise and fall of the meritocracy*. London, UK: Penguin Books.

Zimmerman, B. J., Bandura, A., & Martinez-Pons, M. (1992). Self-motivation for academic attainment: The role of self-efficacy beliefs and personal goal setting. *American Educational Research Journal*. http://doi.org/10.3102/00028312029003663

Zuffianò, A., Alessandri, G., Gerbino, M., Luengo Kanacri, B. P., Di Giunta, L., Milioni, M., & Caprara, G. V. (2013). Academic achievement: The unique contribution of self-efficacy beliefs in self-regulated learning beyond intelligence, personality traits, and self-esteem. *Learning and Individual Differences*, *23*(1), 158–162. http://doi.org/10.1016/j.lindif.2012.07.010

Chapter 2: Genetic influence on social outcomes during and after the Soviet era in Estonia

This chapter, using data from Estonian Genome Centre, University of Tartu, is adapted from a manuscript currently being prepared for submission as a paper to *Nature Human Behaviour.*

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Supplementary materials for this chapter, as detailed in the text, are attached in Appendix 1.

Abstract

The aetiology of individual differences in educational attainment and occupational status includes genetic as well as environmental factors and can change as societies change. The extent of genetic influence on these social outcomes can be viewed as an index of success in achieving meritocratic values of equality of opportunity by rewarding talent and hard work, which are to a large extent influenced by genetic factors, rather than rewarding environmentally driven privilege. To the extent that the end of the Soviet Union and the independence of Estonia led to an increase in meritocratic selection of individuals in education and occupation, genetic influence should be higher in the post-Soviet era than in the Soviet era. Here we confirmed this hypothesis: DNA differences (single-nucleotide polymorphisms, SNPs) explained twice as much variance in educational attainment and occupational status in the post-Soviet era compared to the Soviet era in both polygenic score analyses and SNP heritability analyses of 12,500 Estonians. This is the first demonstration of a change in the extent of genetic influence in the same population following a massive and abrupt social change – in this case, the shift from a communist to a capitalist society. The idea of heritability as an index of equality of opportunity turns current thinking about social mobility on its head.

Introduction

Socioeconomic status (SES), a composite index of educational attainment and occupational status, has been associated with a range of life outcomes from life satisfaction and happiness, to physical and mental health, and even life expectancy (Adler et al., 1994; Batty, Deary, & Gottfredson, 2007; Cutler & Lleras-Muney, 2012; Cutler, Lleras-Muney, & Vogl, 2008; von Stumm, Deary, & Hagger-Johnson, 2013). Individual variation in SES in a population has often been assumed to be explained entirely by environmental factors. Twin and adoption studies, however, suggest that individual differences in SES are substantially genetic in origin (Branigan et al., 2013; Heath et al., 1985; Lykken, Bouchard Jr., McGue, & Tellegen, 1990; Rietveld et al., 2013; Tambs et al., 1989), with heritability estimates from twin studies of about 50%, meaning that around half of the individual differences in SES can be explained by inherited differences in individual's DNA sequence. It is now possible to estimate heritability directly from DNA using hundreds of thousands of DNA differences (single nucleotide polymorphisms, SNPs) genotyped on microarrays (SNP chips) in samples of thousands of unrelated individuals (Yang et al., 2013). Data of this sort are available for many traits, including SES, as a by-product of genome-wide association (GWA) studies. Unlike GWA analysis, which aims to identify specific SNPs associated with a trait, SNP heritability relates overall similarity between individuals across all SNPs on a SNP chip to the individuals' phenotypic similarity on a trait, without knowing which SNPs are associated with the trait.

SNP heritabilities have been estimated for educational attainment, occupational status, and combined SES as about 20% (Benjamin et al., 2012; G. Davies et al., 2016; Hill et al., 2016; Hyytinen, Ilmakunnas, Johansson, & Toivanen, 2013; Marioni et al., 2014; Rietveld et al., 2013). SNP heritability is less than heritability estimates from twin studies because SNP heritability, like GWA analysis, is limited to the additive effects of common SNPs included on SNP chips. For this reason, SNP heritability is the ceiling for GWA studies.

GWA data can also be used to create genome-wide polygenic scores (GPS) that aggregate thousands of SNP associations across the genome. SNP associations typically account for less than 0.1% of the variance, so are not individually useful for prediction. GPS can be created for each individual and correlated with a trait in an independent sample, which could be called *GPS heritability*, the extent to which GPS can explain variance in a trait. A GPS from a GWA study of educational attainment (*EduYears*) (Okbay et al., 2016) predicts 4% of the variance of educational attainment in independent samples (Belsky et al., 2016; Hugh-Jones et al., 2016; Kong et al., 2017; Okbay et al., 2016). No GWA studies of occupational status have been reported, but educational attainment and occupational status correlate about 0.50 phenotypically (Hollingshead, 1975; Sirin, 2005; White, 1982), and the *EduYears* GPS for educational attainment predicts 2% of the variance of occupational status (Belsky et al., 2016), 2% of the variance of SES (Belsky et al., 2016; Domingue, Belsky, Conley, Harris, & Boardman, 2015), and 7% of the variance of family SES using children's DNA (Selzam, Krapohl, et al., 2017). GPS heritability is lower than SNP heritability in part because GPS heritability is limited to specific SNPs shown to be associated with a trait.

Heritability -- including GPS, SNP and twin heritability -- refers to the proportion of individual differences that can be explained by inherited differences in individuals' DNA in a particular population at a particular time. It describes what is, not what could be (Knopik et al., 2017). The reported heritability of educational attainment and occupational status from twin studies differs across birth cohorts and across countries (Baker et al., 1996; Branigan et al., 2013; Colodro-Conde et al., 2015; Heath et al., 1985; Lichtenstein et al., 1992; Okbay et al., 2016; Tambs et al., 1989). Specifically it has been suggested that heritability of educational attainment can change following reform in educational policy (Colodro-Conde et al., 2015; Heath et al., 1985). Higher heritability estimates in twin studies have been noted in countries where educational curriculum is highly standardized, such as the UK, because the standardization reduces environmental differences between schools (Samuelsson et al., 2005). However, research so far has yielded mixed results, with some studies showing change in heritability estimates following a change in curriculum, or changes in the heritability of achievement across birth cohorts, and other studies not showing such an effect (Baker et al., 1996; Branigan et al., 2013; Colodro-Conde et al., 2015). The major limitation to date is that most research has been greatly underpowered; the twin method requires several thousand twin pairs to achieve sufficient power to detect such gene-environment interactions (Hanscombe et al., 2012).

Few studies have investigated changes in SNP heritability as a function of environmental change (Okbay et al., 2016; Rietveld et al., 2013); this method requires several thousand unrelated individuals to detect gene-environment interactions. Only one study has explored secular changes in GPS heritability. Using *EduYears* GPS, GPS heritability of educational attainment was reported to be greater in older as compared to younger cohorts in Sweden (Okbay et al., 2016). This is opposite to the results found in a twin study in Norway (Heath et al., 1985) and also in recent meta-analyses of twin data (Branigan et al., 2013). No evidence has yet been reported for significant changes in GPS or SNP heritability estimates following a major and abrupt social change.

Here we use GPS heritability and SNP heritability to estimate genetic influence on individual differences in educational attainment and occupational status for 12 500 adults participating in the Estonian Genome Centre, University of Tartu (EGCUT). EGCUT affords the unique opportunity to compare heritabilities in a single population before and after the collapse of the Soviet Union. Estonia was occupied by the Soviet Union after World War II and regained independence in 1991 (Laar, 2007a).

The post-Soviet era is generally assumed to be more meritocratic in the sense that access to education and occupation is to a greater extent based on ability (Laar, 2007a, 2007b). Given that education- and occupation-related abilities are substantially due to inherited DNA differences between individuals, greater equality of opportunity implied by meritocracy should diminish the impact of environmental inequalities such as privilege or privation. Inherited DNA differences will remain and will account for a relatively larger portion of differences among individuals. In this sense, heritability can be viewed as an index of equality of opportunity and meritocracy. In a genetically driven meritocracy, genetic differences in ability would account for all individual differences in educational attainment and occupational status. Environmental differences that convey privilege or privation would account for none.

We used the EGCUT sample to test this hypothesis. We compared SNP heritability and GPS heritability for educational attainment and occupational status before and after the collapse of the Soviet Union in Estonia. If independence led to greater meritocracy, the heritability of educational attainment and occupational status should be higher for individuals who lived the majority of their studying and working lives in independent Estonia as compared to those who lived during the Soviet Union.

Materials and Methods

Sample

The sample for the present study was drawn from the Estonian Genome Centre, University of Tartu (EGCUT) sample. EGCUT is a population-based study with a sample size of over 52,000 individuals (all participants ≥18 years of age), which comprises 5% of the adult population in Estonia. Genome-wide genetic data are available for approximately 20,000 of these individuals. EGCUT has been shown to be representative of the Estonian population in terms of age and geographical location while females are overrepresented, 66% female as compared to 55% in the adult population in Estonia (Leitsalu, Haller, et al., 2015). EGCUT is also reasonably representative in terms of educational attainment when compared to the data from the Department of Statistics Estonia (http://www.stat.ee/phc2011) (Supplementary Table 1). The initial sample for the present study included all participants with available genotypic and phenotypic data. All individuals who were 25 or younger were excluded from the analyses, as it is possible that these young individuals had not yet reached their highest educational level and highest occupation. The sample size before exclusions included 17,990 participants (7,409 males and 10,581 females). After exclusions (removing participants who were under 25 at the time of data collection and following quality control) the sample size was reduced to 12,490. Sample size for each measure separately is presented in Supplementary Table 2.

The sample was divided into two historical eras: the Soviet era and the post-Soviet era. Estonia regained independence in 1991, therefore, all participants who were born on or after 1976 went into secondary or further education in the post-Soviet era (they were aged 15 or younger when Estonia regained independence) and the rest of the sample was aged 16 or older when Estonia regained independence. This is an arbitrary cut-off that does not take into account the transition time between communist to capitalist society since the societal changes take time to have an effect on people's lives. We therefore repeated the analyses allowing for a transition period before and after the collapse of the Soviet Union assigning participants who were 16-25 year olds in 1991 to a 'transition' group. In addition, we used another cut-off to define the Soviet and post-Soviet groups, assigning all participants who were aged 10 or younger at the time of the restoration of independence in Estonia to the post-Soviet group and participants who were older than 10 years to the Soviet group.

Measures

Educational attainment

Educational attainment was assessed using a 10-point self-reported scale from no elementary education to postgraduate degree. The measure and scoring followed closely the International

Standard Classification of Education (ISCED: http://www.uis.unesco.org/Education/Pages/international-standard-classification-of-education.aspx). However, some participants were studying towards an undergraduate or postgraduate degree at the time of the data collection, so additional points were added to the scale. Our measure included the following 10 categories (not 8 categories that were in the original scale) for educational attainment: (1) no educational qualifications, (2) elementary school education, (3) basic education/ junior grade of high school, (4) secondary school/high school education, (5) vocational qualification/community college, (6) professional higher education, (7) studying towards university degree, (8) university degree, (9) studying towards postgraduate degree, (10) postgraduate degree. This measure is equivalent to adult years of education phenotype.

Occupational Status

Occupational status was assessed with two questions: "What is your professional status right now?" and "What has been your main professional status (the occupation you kept the longest)?" These occupational status responses were scored according to the International Standard Classifications of Occupations (ISCO: http://www.ilo.org/public/english/bureau/stat/isco/). ISCO is a widely used and reliable measure(H. B. G. Ganzeboom, 2010; H. B. Ganzeboom & Treiman, 2003; Kromhout, 2003; Wolf, 1997). ISCO classification assigns occupational status to broad groups (as well as more specific subgroups), taking into account the skills and education level required for occupation as well as the potential earnings. The present study used nine occupational status groups, classified in ISCO as the following categories, scored from 1 to 9 respectively: (1) elementary occupations (cleaners, helpers, laborers), (2) plant and machine operators, assemblers, (3) craft and related trades workers, (4) skilled agricultural, forestry and fishery workers, (5) service and sales workers, (6) clerical support workers, (7) technicians and associate professionals, (8) professionals, (9) legislators, senior officials and managers. The current occupational status and the main occupational status correlated 0.46. Both the current and the main occupational status had missing data; therefore, to increase power and sample size, a composite measure of occupational status was created by taking the mean of current and the longest held occupations; if only one measure was available then that measure was used.

SES

Socio-economic status (SES) was calculated as the mean of educational attainment and occupational status, which correlated 0.62. Although this measure of SES does not include family income, occupational classification takes into account the potential earnings and prestige of the occupation. Therefore, we consider the SES measure combined from occupational status and educational attainment to be a reasonable measure of SES.

Height and weight

Height and weight were used as control variables in the analyses; we had no hypothesis about changes in the SNP or GPS heritabilities following the shift from a communist to a capitalist society. Height and weight were assessed in person by the researchers. Height was measured in cm and weight was measured in kg.

Genotyping

Venous blood was collected from all 52,000 participants of EGCUT. DNA and plasma were immediately extracted from the blood and stored in EGCUT Core Laboratory of EGCUT in Tartu, Estonia. Genome-wide genotyping was assayed for 20,000 participants using three Illumina arrays: Illumina HumanCoreExome, Illumina Human370 CNV and Illumina OmniExpress in the Core Laboratory of EGCUT in Tartu, Estonia.

Quality Control

Genotype quality control and filtration were performed using Illumina GenomeStudio 3.1 and PLINK 1.07 (Purcell et al., 2007). Standard quality control analyses were conducted at both the individual level and the SNP level excluding individuals with genotype call rate < 95%, sex discrepancies (using the heterozygosity rate of X-chromosome) and excess heterozygosity (mean±3SD). Additionally, duplicates and multidimensional-scaling (MDS) outliers were excluded. At the SNP level, we excluded SNPs with minor allele frequency (MAF) < 1%, call rate < 95%, failure of the Hardy-Weinberg Equilibrium (HWE) exact test (threshold $1*10^{-6}$), A/T or C/G and sex chromosome SNPs were removed. Phasing and imputation of the cleaned data was performed using ShapeIT v2 (Delaneau, Zagury, & Marchini, 2013) and IMPUTE v2.3.1 (Howie, Donnelly, & Marchini, 2009) with 1000 Genomes Phase 3 Oct 2014 imputation reference panel based on 5 008 haplotypes[4] (www.1000genomes.org). IMPUTE2 builds custom-reference panels for each individual to be imputed and so is the best-suited software for imputing genotype data from Estonians, for whom no population-specific reference panel exists.

After imputation, further quality control was carried out. SNPs with MAF < 1%, and SNPs with poor imputation quality (info score < 0.30) or failure of the HWE exact test (threshold $1*10^{-6}$) were removed. We harmonized the genotyped datasets across the 3 arrays removing duplicate individuals and duplicate markers. Other standard quality control methods were applied removing SNPs and samples with call rate <0.97. The quality control was performed on each array separately, and was repeated after harmonization. After harmonization and quality control the final sample included 4,052,281 variants and 16,397 individuals.

To control for ancestral stratification, principal component analyses were performed after pruning to remove markers in linkage disequilibrium (200kb window using $R^2 > 0.05$). The first 10 principal components were used as covariates in the genetic analyses.

Statistical Analyses

Means and variances for measures were calculated, comparing the Soviet era and post-Soviet era, as well as sex differences. Mean differences were tested using ANOVA (Supplementary Table 2). Because significant, though small, sex differences emerged for both occupational status and educational attainment, explaining 2-4% of the variance in SES measures, we corrected the measures for mean sex differences using the regression method. In addition, we repeated the analyses without sex correction and calculated the variance explained by GPSs created separately for males and females. No correction for multiple testing was done, as all analyses tested just one hypothesis and we were interested in the effect size rather than the significance level.

Genome-wide polygenic scores

Genome-wide polygenic scores (GPSs) aggregate the effects of individual SNPs shown to be associated with the trait in a GWA study (Dudbridge, 2013). GPSs were calculated for 16 398 participants using p-values and β- weights obtained from summary statistics from Okbay et al 2016 Years of Education (*EduYears*) GWA analysis (Okbay et al., 2016) with the PRSice program (Euesden, Lewis, & O'Reilly, 2014) using multiple p-value thresholds (0.001; 0.05; 0.1; 0.2; 0.3; 0.4; 0.5). Of the 293,723 participants in the *EduYears* GWAS, the present study excluded 23andMe participants, for legal reasons, and excluded all participants from EGCUT, resulting in a sample of 208 596 individuals (See Supplementary Table 3 for cohort description). SNPs were clumped in PRSice for linkage disequilibrium, using a cut-off of R^2=0.1 within a 250-kb window. GWA summary statistics were obtained from the sample of 208,596 individuals, and p-values and β- weights were used to calculate the *EduYears* GPS. Delta R^2 are reported as the estimates of variance explained by adding the GPS to the regression model that only included 10 principal components that controlled for population stratification.

SNP heritability

SNP heritability estimates genetic and residual (environmental) components of variance directly from DNA using unrelated individuals and hundreds of thousands of SNPs (single nucleotide polymorphisms) from thousands of individuals (Yang et al., 2010). Using GCTA software, a genetic relatedness matrix was calculated weighting the pairwise genetic similarities with allele frequencies across all genotyped SNPs (Yang et al., 2010, 2011). Individuals found to be even remotely related (relatedness >0.05) were removed from the analyses. We repeated the analyses when using the more stringent cut-off of 0.025, but this did not make any difference in SNP heritability estimates. This matrix of pair-by-pair genetic similarities was then compared to the matrix of pair-by-pair phenotypic similarity using residual maximum likelihood estimation (Yang et al., 2010, 2011). This method only assesses additive effects captured by the common SNPs genotyped on the DNA array, and does not take into account gene-gene or gene-environment interactions or rare DNA variants, but these are unlikely to have a strong influence on the phenotype (Visscher et al., 2008; Yang et al., 2010). Prior to SNP heritability analyses we adjusted educational attainment and occupational status for sex using regression; standardized residuals were used in all analyses. To correct for the slight skew in the data, all measures were transformed to a normal distribution using the van der Waerden rank-based transformation (Lehmann, 1975; Van Der Waerden BL, 1975).

Statistical power

Power for estimating GPS heritability was estimated using the online tool GCTA-GREML power calculator (Visscher et al., 2014) and AVENGEME R code (Dudbridge, 2013; Palla & Dudbridge, 2015). Our sample provided more than 80% power to detect 4% variance explained by GPS under the following circumstances: GWAS discovery sample size 208 596 in our target sample including 12 500 participants (the power did not change when we calculated power with 2100 target sample or 680 target sample for post-Soviet subgroups); number of independent SNPs in the GPS=20,000; proportion of variance explained in discovery sample =4%, covariance between genetic effect sizes in the discovery and target sample 4%; proportion of SNPs with no effects on discovery trait=99%; range of p-values from GWA summary statistics= 0.00- 0.5). The difference in GPS heritabilities was calculated using Fisher's exact test with Z to r transformation that assesses the significance in the difference in correlation coefficients in independent samples using both the effect sizes and sample sizes in the two samples (Fisher, 1921).

Power for estimating SNP heritability is 99% to detect a SNP heritability of 20% for the whole sample. For the Soviet-era subsample, we had 99% power to detect a SNP heritability of 20%, but power was only 24% in the post-Soviet era (the power to detect heritability of 35% was 64% in the post Soviet era). Therefore, little confidence is warranted for assessing differences in SNP heritability in the Soviet and the post-Soviet groups.

Results

Descriptive statistics

Means and standard deviations were calculated for height, weight, educational attainment, occupational status and SES for the whole sample, males and females separately and for historical eras separately. ANOVA results show that historical group and sex explained up to 4% variance in SES variables (see Supplementary Table 2 for details). For subsequent analyses, we controlled for sex effects by using sex-regressed standardized residuals.

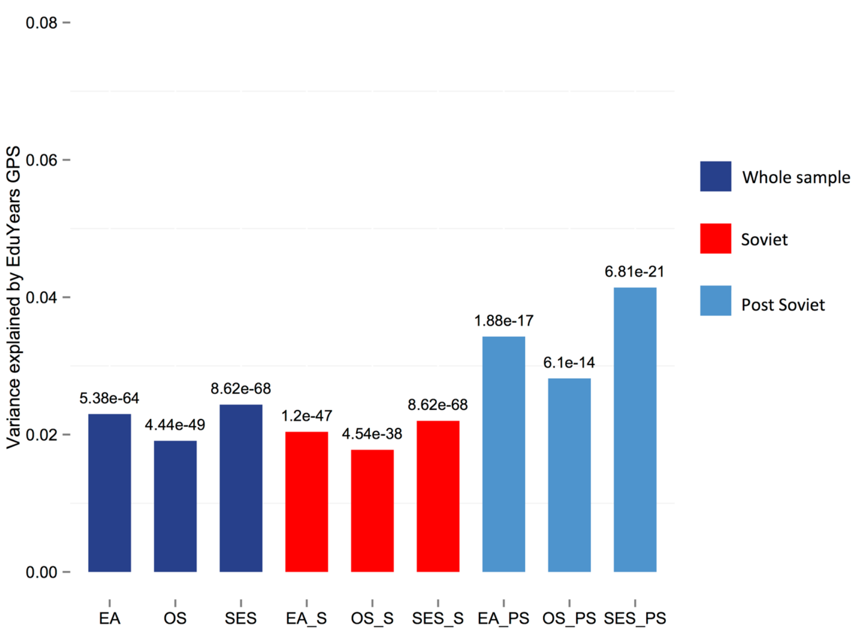
GPS heritability

EduYears GPS was used to compare GPS heritability in the Soviet and post-Soviet eras. For the whole sample, GPS heritabilities were 2.4% for SES, 1.9% for occupational status, and 2.3% for educational attainment (Figure 1). GPS heritabilities were greater in the post-Soviet era for all three measures.

Using the less stringent cut-off of 15 years (Figure 1a), GPS heritabilities for SES were significantly greater for the post-Soviet era (4.1%) compared to the Soviet era (2.2%) (Fisher's r-to-z test: z=2.38, p=0.017). (See Supplementary Table 4 for all comparisons.) These results are based on a GPS calculated at a 0.1 GWA study p-value threshold, which provided the best prediction. (Supplementary Figure 1 shows variance explained across multiple thresholds.)

The more stringent cut-off of 10 years yielded stronger results (Figure 1b). For SES, GPS heritability was significantly greater in the post-Soviet era (7.5%) compared to the Soviet era (2.3%) (Fisher's r-to-z test: z=5.29, p<0.001). (See Supplementary Table 4 for all comparisons.) GPS heritability was also significantly greater in the post-Soviet era compared to the Soviet era for occupational status, GPS heritabilities were 1.7% (Soviet) and 5.6% (post Soviet), and for educational attainment GPS heritabilities were 2.1% (Soviet) and 6.1% (post Soviet).

a)



b)

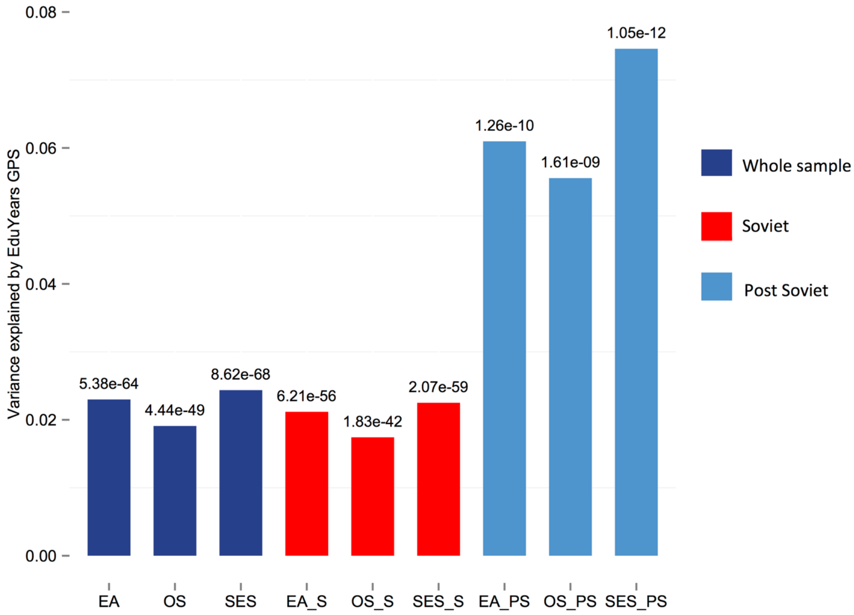


Figure 1. Variance explained by *EduYears* GPS calculated at a 0.1 GWA study p-value threshold for educational attainment (EA), occupational status (OS) and SES for the whole EGCUT sample and when divided into historical eras using two cut-offs: (a) The post-Soviet (PS) group included participants 15 or younger when independence was regained and the Soviet (S) group included the rest of the participants; (b) The post-Soviet (PS) group included participants 10 or younger when independence was regained and the Soviet (S) group included the rest of the participants.

The estimates for SES in the post-Soviet era are in line with the estimates obtained in the UK (Selzam, Krapohl, et al., 2017) for family SES using offspring GPS, while significantly less variance was explained by the GPS scores in the Soviet era. Additional analyses were run using variables that were not sex corrected (Supplementary Figure 2) and taking the transition period between Soviet and post-Soviet era into account (Supplementary Figure 3) and the results remained very similar. The proportion of variance explained by GPS was also calculated for males and females separately (Supplementary Figure 4). The difference between the variance explained by *EduYears* GPS in the

Soviet and post-Soviet era was significantly larger for females compared to males, further suggesting increased meritocracy after the Soviet era.

We divided the sample into birth cohorts (10-year and 5-year intervals) to check whether the variance explained by GPS is simply explained by the birth cohort (Supplementary Figure 5). While the variance explained fluctuates across birth cohorts, this did not explain the increased proportion of variance explained by GPS after the restoration of independence in Estonia. (See Supplementary Figure 6 for distribution of SES for the Soviet and post-Soviet groups and Supplementary Figure 7 for distribution of *EduYears* GPS for the Soviet and post-Soviet groups.)

We also used height as a control variable. *EduYears* GPS explained less than 1% of the variance in height regardless of the historical era (Supplementary Figure 8). This slight association is to be expected because height correlates significantly but slightly with SES variables. For example, the genetic correlation between household income (a good proxy for SES) and height has been shown to be around 0.2 (Hill et al., 2016).

SNP heritability

SNP heritabilities for educational attainment and occupational status were calculated for the whole sample and for the Soviet and post-Soviet groups. For the whole sample, SNP heritabilities were 19% (SE 0.03) for the SES composite, 15% (SE 0.03) for occupational status and 18% (SE 0.03) for educational attainment (Figure 2). Similar to the GPS heritabilities, SNP heritabilities were almost twice as high in the post-Soviet than the Soviet era using age 15 as a cut-off, which yields the largest post-Soviet group (Figure 2). In the Soviet era, SNP heritabilities were 17% (SE 0.04) for SES, 17% (SE 0.04) for occupational status, and 18% (SE 0.04) for educational attainment. After the Soviet era, SNP heritabilities were 38% (SE 0.15), 23% (SE 0.16) and 37% (SE 0.14), respectively. The SNP heritabilities are larger in the post-Soviet era for SES and educational attainment but not for occupational status, however, this difference was not significantly different as is evident from the standard error bars in Figure 2.

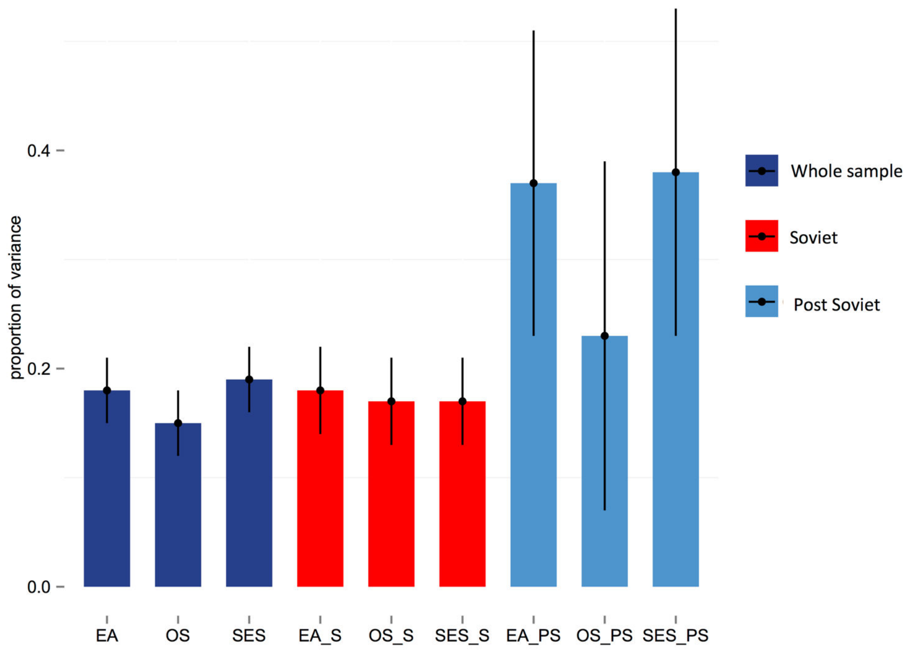


Figure 2. SNP heritabilities showing the proportion of variance explained by additive effects of common SNPs (SE as error bars) for the whole EGCUT sample and for the Soviet and post-Soviet groups using a cut-off of 15 years. SNP heritabilities were adjusted for population stratification.

Height and weight were also used as control variables for analyses of SNP heritabilities. SNP heritabilities were 32% for height and 21% for weight in the whole sample. For the Soviet era, SNP heritabilities were 33% for height and 21% and weight. The post-Soviet estimates were not significantly different: 40% for height and 22% for weight (Supplementary Figure 9).

Discussion

Our novel finding is that both GPS and SNP heritabilities are about twice as high for SES in the post-Soviet era in the same Estonian sample. Although previous studies have reported differences in heritabilities across birth cohorts (Branigan et al., 2013; Okbay et al., 2016), in the present study the greater heritability in the post-Soviet era was not simply a birth-cohort difference.

A possible explanation for the increased heritability is increased meritocracy in Estonia following the restoration of independence in Estonia. By meritocracy, we refer to equal opportunity for access to education and occupation and, when selection occurs, to meritocratic selection based on talent and effort, which are substantially influenced by genetic factors, rather than on environmentally driven privilege or discrimination. A meritocratic mechanism for the increased heritability of educational attainment and occupational status in the post-Soviet era could be genotype-environment correlation in the sense that individuals with equal opportunities are better able to select or to be selected for educational and occupational environments correlated with their genetic propensities. When environmental differences in access to education and occupation diminish, genetic differences increasingly account for educational attainment and occupational status.

There are of course other possible explanations for increased GPS heritability in post-Soviet era. Much has changed in the society after the collapse of the Soviet Union, including wealth, culture, values -- all of which might contribute to the change in GPS heritability for the cohort who lived, studied and worked the majority of their lives in independent Estonia. However, we see no specific hypothesis about the increased heritability following the collapse of the Soviet Union as obvious as increased meritocracy.

Another possible explanation is methodological. GPS scores were calculated for *EduYears* on the basis of a meta-analytic GWA of heterogeneous cohorts. If the GWA discovery sample weights were closer to the post-Soviet sample in the present study, then more variance would be explained in the post-Soviet compared to Soviet sample.

Equal educational opportunities

In the Soviet era, access to primary and secondary education was universal, and universal secondary education was introduced in 1960s. However, the quality of teaching and even the curricula varied widely across schools (Saar, 1997, 2010). Within schools, students were divided into one of the three different tracks, with limited movement between tracks: vocational training, secondary education and (special) secondary education (Titma, Tuma, & Roosma, 2003). This tracking was partly done based on merit (school achievement), but social-political ranking played a significant part as well. The number of students admitted to each track depended on economic and social goals of central planning at the time; individual aspirations and ability were not considered to be as important (Saar, 1997). Access to tertiary education from lower 'ranks' in the social-political system was limited; students who were religious were not admitted (Saar, 2010; Titma et al., 2003). In this way, the Soviet education system created environmental inequalities both directly and indirectly (Saar, 1997). Importantly, university education was not as highly valued in society as it is now and this was accompanied by limited competition for university places, with an average of only two applicants per position. Admissions to university remained low throughout the Soviet era, which restricted any selection, meritocratic or not.

Since regaining independence, education in Estonia has become more meritocratic in terms of educational opportunity. Many educational reforms were introduced after the collapse of the Soviet Union with the aim of building a more egalitarian and effective educational system. Currently, almost everybody completes elementary education and the rate of completing secondary education is among the highest in the OECD countries. Equality education in Estonia is now above the OECD average, with limited variation in teaching standards between schools. The quality of teaching is considered to be excellent according to international standards and Estonia is ranked among the highest performing educational systems according to PISA surveys in 2012 and 2015 (OECD, 2011, 2016). This overall educational excellence, and the limited number of selective or private schools, suggests that there is equal opportunity and access to good education for all at primary and secondary level of education. We hypothesized that equality of opportunity should increase the heritability of educational achievement by making it possible for children to select, modify and choose educational experiences correlated with their education-related genetically influenced propensities, which include appetites as well as abilities. Educational achievement contributes importantly to educational attainment and occupational status.

For tertiary education, in addition to self-selection, students are now selected for university largely on the basis of ability and prior achievement, rather than environmentally driven privilege. Selection is not based on socio-political or religious considerations as in the Soviet era. Nor is selection based on the ability to pay tuition, because almost all university education is free. There is greater opportunity for selection for university admission in the post-Soviet era because university applications and admissions increased exponentially in the 1990s; for example, admissions to University of Tartu have increased threefold compared to the Soviet era (Saar, 2010).

Equal access to occupation

During the Soviet era, the economy and labour market was mainly characterized by centralized control, with the majority of the workforce assigned to jobs in manufacturing and agriculture. Occupational status was determined more by loyalty to the communist party than by ability, achievement or qualifications. Recommendations for job positions and promotion always came from party leaders, although educational qualifications were also needed for certain positions (Titma & Roots, 2006). The economy and labour market had very limited mobility of the workforce (Titma et al., 2003).

Inequality in occupations during the Soviet era was even more dramatic for females than males. During the Soviet era there was an increase in participation of women in workforce, meaning that both men and women were largely employed. However, this did not lead to occupational equality; women often did jobs requiring lower level of skills (Carnaghan & Bahry, 1990). Although Soviet ideology argued for gender equality, this was not carried out in practice (Katz, 2001).

The transition from the Soviet Union to a prosperous independent Estonia was more difficult than anticipated. After the restoration of independence in Estonia the living standards were low, the economy was struggling, and the situation worsened with a major recession until 1994 when Estonia joined the European Union (Laar, 2007a, 2007b). Equality of opportunity increased as the former Soviet Estonia became more integrated with the west (Boughton, 2012).

These historical events may explain why *EduYears* GPS did not explain more variance in SES in the transition time compared to the Soviet era. Our results suggested that *EduYears* GPS heritability is greatest for the youngest participants who had lived, studied and worked in independent Estonia the longest.

Gender equality in Estonia started to improve, albeit gradually, after the collapse of the Soviet Union (Silova & Magno, 2004). This was mirrored by an interesting facet of the results in the present study showing that GPS heritability increased more dramatically for females compared to males following the collapse of the Soviet Union. These results further support the meritocratic hypothesis specifically in relation to gender.

Future research directions

The present analyses excluded participants who were younger than 25 at the time of data collection because they may not yet have achieved their highest educational qualifications or reached their highest occupational status. Linking the EGCUT database with data from the Estonian Department of Education will make it possible in the future to include these individuals as they complete their education and reach their ultimate occupational status. This will increase the size of our post-Soviet sample and thus the power of our SNP and GPS heritability comparisons. Because these individuals grew up completely in the post-Soviet era, we would predict that they show even greater heritability of SES.

Another interesting direction for research concerns the relationship between education and fecundity. Decreased fecundity in Iceland among highly educated citizens has been reported to result in lower GPS scores for *EduYears,* although the effect is very small (Kong et al., 2017). According to Statistics Estonia, the population in Estonia has been decreasing for decades (http://www.stat.ee/news-release-2017-008), although it increased for the first time in 2016. We plan to investigate the extent to which decreasing fecundity comes disproportionately from highly educated individuals, in which case we might expect lower average GPS in the most recent birth cohorts. Our preliminary analyses did not support this hypothesis in that the average *EduYears* GPS did not differ across birth cohorts (Supplementary Figure 10), although we did not study fecundity here.

Studying parent-offspring resemblance is also part of our future research plans in EGCUT in order to study intergenerational social mobility. Intergenerational social mobility is often assumed to be solely due to environmental factors. For example, the OECD uses parent-offspring resemblance in SES outcomes to assess intergenerational social mobility, assuming that this resemblance is environmentally mediated. Our current results and results from other studies show that educational and occupational outcomes are partly explained by genetic factors. Because parents and offspring are on average 50% similar genetically, parent-offspring resemblance is also likely to show genetic influence for SES. From this perspective, parent-offspring resemblance could be viewed as an index of equality rather than inequality. In other words, if environmental inequalities were eliminated, genetic resemblance between parents and offspring would completely account for parent-offspring resemblance.

While our analyses provided evidence for changes in GPS and SNP heritabilities following the major social change from a communist to a capitalist society, no definite conclusions can be drawn. It is necessary to replicate the results of the present analyses using data from a different country that has gone though similar abrupt social change. A country that used to be part of the Soviet Union and has regained independence would be ideal, however, we are not aware of an available replication sample at this time. We hope that our results lead to future molecular genetic studies researching gene-environment interactions of this sort that are now possible using GPS scores.

Another direction for future research is to consider intermediate phenotypes such as cognitive abilities that might mediate these changes in the distal outcomes of educational attainment and occupational status. In addition, the precision and power of all of these SNP and GPS analyses will increase as the power of GWA studies increases.

Meritocracy or social justice?

In closing, we wish to emphasize that we are not advocating meritocracy. Although at first glance meritocracy seems unquestionably good, it could have unintended consequences such as creating social inequalities if societal rewards such as wealth are doled out on the basis of genetically driven abilities. The word meritocracy was coined by Michael Young whose book, *The Rise and Fall of the* Meritocracy (Young, 1965), was meant as a cautionary tale about the dangers of meritocracy. We agree with the counterargument that the focus should be on social justice not meritocracy (Bloodsworth, 2016). That is, we can deny the value system that drives the debate about meritocracy. This value system assumes that the point of education is to get better test scores in order to get better jobs, and that the point of occupations is to achieve high status and make lots of money. A different way to look at education is as a time to learn basic skills but also to learn how to learn and to enjoy learning. It is a decade when children can find out what they like to do and what they are good at doing, finding their genetic selves. Learning is for everyone but not everyone is for university.

Similarly with occupations, where selection cannot be avoided, we will end up with a lot of frustrated people if we only value high-status occupations that earn lots of money. Society needs people who are good care workers, nurses, plumbers, public servants, and people in the service industry. We can deny the value system based on money. Society could choose to reduce income inequality with a tax system that redistributes wealth.

In his book, *The Myth of Meritocracy,* James Bloodworth (2016) suggests that we need to replace meritocracy with a just society. He argues that meritocracy promotes genetic inequality, which leads to an inherent inequality of opportunity. Economic inequality needs to be tackled directly through taxation to reduce the gap between rich and poor. People are more concerned with fairness, a just society, than with economic inequality per se. The most quoted statistic from Thomas Piketty's high-profile book, *Capital in the Twenty-first Century,* is that 60% of the increase in US national income in the last three decades went to just the top 1% of earners, primarily due to soaring salaries at the top end of the pay scale (Piketty, 2014). We suggest that more important than the relative inequality of income for this top 1% is the absolute inequality of the bottom third whose debts exceed their assets.

References

Adler, N. E., Boyce, T., Chesney, M. A., Cohen, S., Folkman, S., Kahn, R. L., & Syme, S. L. (1994). Socioeconomic status and health: the challenge of the gradient. *American Psychologist*, *49*(1), 15–24. http://doi.org/http://dx.doi.org/10.1016/B0-08-043076-7/03827-4

Baker, L. A., Treloar, S. A., Reynolds, C. A., Heath, A. C., & Martin, N. G. (1996). Genetics of educational attainment in Australian twins: Sex differences and secular changes. *Behavior Genetics*, *26*(2), 89–102. http://doi.org/10.1007/BF02359887

Batty, G. D., Deary, I. J., & Gottfredson, L. S. (2007). Premorbid (early life) IQ and Later Mortality Risk: Systematic Review. *Annals of Epidemiology*, *17*(4), 278–288. http://doi.org/10.1016/j.annepidem.2006.07.010

Belsky, D. W., Moffitt, T. E., Corcoran, D. L., Domingue, B., Harrington, H., Hogan, S., … Caspi, A. (2016). The genetics of success: how single-nucleotide polymorphisms associated with educational attainment relate to life-course development. *Psychological Science*, *27*, 957–972. http://doi.org/10.1177/0956797616643070

Benjamin, D. J., Cesarini, D., van der Loos, M. J. H. M., Dawes, C. T., Koellinger, P. D., Magnusson, P. K. E., … Visscher, P. M. (2012). The genetic architecture of economic and political preferences. *Proceedings of the National Academy of Sciences*, *109*, 8026–8031. http://doi.org/10.1073/pnas.1120666109

Bloodsworth, J. (2016). *The myth of meritocracy*. Biteback Publishing, London, UK.

Boughton, J. (2012). *Tearing Down Walls: The International Monetary Fund, 1990-1999*. Washington, DC.

Branigan, A. R., Mccallum, K. J., & Freese, J. (2013). Variation in the heritability of educational attainment: An international meta-analysis. *Social Forces*, *92*(1), 109–140. http://doi.org/10.1093/sf/sot076

Carnaghan, E., & Bahry, D. (1990). Political Attitudes and the Gender Gap in the USSR. *Comparative Politics*, *22*(4), 379–399. http://doi.org/10.2307/421970

Colodro-Conde, L., Rijsdijk, F., Tornero-Gómez, M. J., Sánchez-Romera, J. F., & Ordoñana, J. R. (2015). Equality in educational policy and the heritability of educational attainment. *PLoS ONE*, *10*(11), e0143796. http://doi.org/10.1371/journal.pone.0143796

Cutler, D. M., & Lleras-Muney, A. (2012). *Education and health: insights from international comparisons* (No. 17738). *NBER Working Papers*.

Cutler, D. M., Lleras-Muney, A., & Vogl, T. (2008). *Socioeconomic status and health: dimensions and mechanisms* (No. 14333). *NBER Working Papers*.

Davies, G., Marioni, R. E., Liewald, D. C., Hill, W. D., Hagenaars, S. P., Harris, S. E., … Deary, I. J. (2016). Genome-wide association study of cognitive functions and educational attainment in UK Biobank (N=112 151). *Molecular Psychiatry*, *21*(6), 758–67. http://doi.org/10.1038/mp.2016.45

Delaneau, O., Zagury, J.-F., & Marchini, J. (2013). Improved whole-chromosome phasing for disease and population genetic studies. *Nature Methods*, *10*(1), 5–6. http://doi.org/10.1038/nmeth.2307

Domingue, B. W., Belsky, D. W., Conley, D., Harris, K. M., & Boardman, J. D. (2015). Polygenic influence on educational attainment. *AERA Open*, *1*(3), 2332858415599972. http://doi.org/10.1177/2332858415599972

Dudbridge, F. (2013). Power and predictive accuracy of polygenic risk scores. *PLoS Genetics*, *9*(3), e1003348. http://doi.org/10.1371/journal.pgen.1003348

Euesden, J., Lewis, C. M., & O'Reilly, P. F. (2014). PRSice: Polygenic Risk Score software. *Bioinformatics*, *31*(9), 1466–1468. http://doi.org/10.1093/bioinformatics/btu848

Fisher, R. (1921). On the probable error of a coefficient of correlation deduced from a small sample. *Metron*, *1*, 3–32.

Ganzeboom, H. B. G. (2010). A New International Socio-Economic Index [ISEI] of occupational status for the International Standard Classification of Occupation 2008 [ISCO-08] constructed with data from the ISSP 2002-2007; with an analysis of quality of occupational measurement in ISS. *Annual Conference of International Sociall Survey Programme , Lisbon.*

Ganzeboom, H. B., & Treiman, D. J. (2003). Three internationally standardised measures for comparative research on occupational status. In J. H. P. Hoffmeyer-Zlotnik & Christof Wolf (Eds.), *Advances in Cross-National Comparison. A European Working Book for Demographic and Socio-Economic Variables.* (pp. 159–193). New York: Kluwer Academic Press.

Hanscombe, K. B., Trzaskowski, M., Haworth, C. M. A., Davis, O. S. P., Dale, P. S., & Plomin, R. (2012). Socioeconomic status (SES) and children's intelligence (IQ): in a UK-representative sample SES moderates the environmental, not genetic, effect on IQ. *PloS One*, *7*(2), e30320. http://doi.org/10.1371/journal.pone.0030320

Heath, A. C., Berg, K., Eaves, L. J., Solaas, M. H., Corey, L. A., Sundet, J., … Nance, W. E. (1985). Education policy and the heritability of educational attainment. *Nature*. http://doi.org/10.1038/314734a0

Hill, W. D., Hagenaars, S. P., Marioni, R. E., Harris, S. E., Liewald, D. C., Davies, G., … Deary, I. J. (2016). Molecular genetic contributions to social deprivation and household income in UK Biobank (n = 112,151). *Current Biology*, *26*(22), 3083–3089. http://doi.org/10.1101/043000

Hollingshead, A. (1975). Four factor index of social status. *Yale Journal of Sociology*.

Howie, B. N., Donnelly, P., & Marchini, J. (2009). A flexible and accurate genotype imputation method for the next generation of genome-wide association studies. *PLoS Genetics*, *5*(6), e1000529. http://doi.org/10.1371/journal.pgen.1000529

Hugh-Jones, D., Verweij, K. J. H., St. Pourcain, B., & Abdellaoui, A. (2016). Assortative mating on educational attainment leads to genetic spousal resemblance for polygenic scores. *Intelligence*, *59*, 103–108. http://doi.org/10.1016/j.intell.2016.08.005

Hyytinen, A., Ilmakunnas, P., Johansson, E., & Toivanen, O. (2013). *Heritability of lifetime income* (No. 364). *Helsinki Centre of Economic Research*.

Katz, K. (2001). *Gender, work and wages in the Soviet Union: a legacy of discrimination*. Palgrave Macmillan UK.

Knopik, V. S., Neiderhiser, J. M., DeFries, J. C., & Plomin, R. (2017). *Behavioral Genetics. 7th ed*. Worth Publishers, New York.

Kong, A., Frigge, M. L., Thorleifsson, G., Stefansson, H., Young, A. I., Zink, F., … Stefansson, K. (2017). Selection against variants in the genome associated with educational attainment. *Proceedings of the National Academy of Sciences*, *114*(5), E727-32. http://doi.org/10.1073/pnas.1612113114

Kromhout, H. (2003). The use of occupation and industry classifications in general population studies. *International Journal of Epidemiology*, *32*(3), 419–428. http://doi.org/10.1093/ije/dyg080

Laar, M. (2007a). *Estonia's way*. Tallinn, Estonia: Pegasus, Tallinn, Estonia.

Laar, M. (2007b). The Estonian economic miracle. *Backgrounder*, *2060*, 1–12.

Lehmann, E. (1975). *Nonparametric Statistical Methods Based on Ranks*. Holden-Day, San Francisco, CA.

Leitsalu, L., Haller, T., Esko, T., Tammesoo, M. L., Alavere, H., Snieder, H., … Metspalu, A. (2015). Cohort profile: Estonian Biobank of the Estonian Genome Center, University of Tartu. *International Journal of Epidemiology*, *44*(4), 1137–1147. http://doi.org/10.1093/ije/dyt268

Lichtenstein, P., Pedersen, N. L., & McClearn, G. E. (1992). The Origins of Individual Differences in Occupational Status and Educational Level: A Study of Twins Reared Apart and Together. *Acta Sociologica*, *35*(1), 13–31. http://doi.org/10.1177/000169939203500102

Lykken, D. T., Bouchard Jr., T. J., McGue, M., & Tellegen, A. (1990). The Minnesota Twin Family Registry: some initial findings. *Acta Genet Med Gemellol*, *39*(1), 35–70. http://doi.org/10.1017/S0001566000005572

Marioni, R. E., Davies, G., Hayward, C., Liewald, D., Kerr, S. M., Campbell, A., … Deary, I. J. (2014). Molecular genetic contributions to socioeconomic status and intelligence. *Intelligence*, *44*, 26–32. http://doi.org/10.1016/j.intell.2014.02.006

OECD. (2011). *Equity and Quality in Education - Supporting Disadvantaged Students and Schools*.

OECD. (2016). *Education Policy Outlook: Estonia*.

Okbay, A., Beauchamp, J. P., Fontana, M., Lee, J. J., Pers, T. ., Rietveld, C. A., … Pickrell, J. K. (2016). Genome-wide association study identifies 74 loci associated with educational attainment. *Nature*, *533*(7604), 539–542. http://doi.org/10.1038/nature17671

Palla, L., & Dudbridge, F. (2015). A fast method that uses polygenic scores to estimate the variance explained by genome-wide marker panels and the proportion of variants affecting a trait. *American Journal of Human Genetics*, *97*(2), 250–259. http://doi.org/10.1016/j.ajhg.2015.06.005

Piketty, T. (2014). *Capital in the twenty-first century*. Harvard, US: Harvard University Press.

Purcell, S., Neale, B., Todd-Brown, K., Thomas, L., Ferreira, M. A. R., Bender, D., … Sham, P. C. (2007). PLINK: A tool set for whole-genome association and population-based linkage analyses. *American Journal of Human Genetics*, *81*(3), 559–575. http://doi.org/10.1086/519795

Rietveld, C. A., Medland, S. E., Derringer, J., Yang, J., Esko, T., Martin, N. W., … Koellinger, P. D. (2013). GWAS of 126,559 individuals identifies genetic variants associated with educational attainment. *Science*, *340*(6139), 1467–71. http://doi.org/10.1126/science.1235488

Saar, E. (1997). Transitions to Tertiary Education in Belarus and the Baltic Countries. *European Sociological Review*, *13*(2), 139–158. http://doi.org/https://doi.org/10.1093/oxfordjournals.esr.a018209

Saar, E. (2010). Changes in intergenerational mobility and educational inequality in Estonia: Comparative analysis of cohorts born between 1930 and 1974. *European Sociological Review*, *26*(3), 367–383. http://doi.org/10.1093/esr/jcp049

Samuelsson, S., Byrne, B., Quain, P., Wadsworth, S., Corley, R., DeFries, J. C., … Olson, R. (2005). Environmental and genetic influences on prereading skills in Australia, Scandinavia, and the United States. *Journal of Educational Psychology*. http://doi.org/10.1037/0022-0663.97.4.705

Selzam, S., Krapohl, E., von Stumm, S., O'Reilly, P. F., Rimfeld, K., Kovas, Y., … Plomin, R. (2017).

Predicting educational achievement from DNA. *Molecular Psychiatry*, *22*, 267–272. http://doi.org/10.1038/mp.2016.107

Silova, I., & Magno, C. (2004). Gender equity unmasked: democracy, gender, and education in Central/Southeastern Europe and the former Soviet Union. *Comparative Education Review*, *48*(4), 417–442. http://doi.org/10.1086/423358

Sirin, S. R. (2005). Socioeconomic Status and Academic Achievement: A Meta-Analytic Review of Research. *Review of Educational Research*, *75*(3), 417–453. http://doi.org/10.3102/00346543075003417

Tambs, K., Sundet, J. M., Magnus, P., & Berg, K. (1989). Genetic and environmental contributions to the covariance between occupational status, educational attainment, and IQ: A study of twins. *Behavior Genetics*, *19*(2), 209–222. http://doi.org/10.1007/BF01065905

Titma, M., & Roots, A. (2006). Intragenerational Mobility in Successor States of the USSR. *European Societies*, *8*(4), 493–526. http://doi.org/10.1080/14616690500342618

Titma, M., Tuma, N. B., & Roosma, K. (2003). Education as a Factor in Intergenerational Mobility in Soviet Society. *European Sociological Review*. http://doi.org/10.1093/esr/19.3.281

Van Der Waerden BL. (1975). On the sources of my book Moderne Algebra. *Historia Mathematica*, *2*(1), 31–40.

Visscher, P. M., Hemani, G., Vinkhuyzen, A. A. E., Chen, G. B., Lee, S. H., Wray, N. R., … Yang, J. (2014). Statistical Power to Detect Genetic (Co)Variance of Complex Traits Using SNP Data in Unrelated Samples. *PLoS Genetics*, *10*(4), e1004269. http://doi.org/10.1371/journal.pgen.1004269

Visscher, P. M., Hill, W. G., & Wray, N. R. (2008). Heritability in the genomics era — concepts and misconceptions. *Nature Reviews Genetics*, *9*(4), 255–266. http://doi.org/10.1038/nrg2322

von Stumm, S., Deary, I. J., & Hagger-Johnson, G. (2013). Life-course pathways to psychological distress: a cohort study. *BMJ Open*, *3*(5), e002772. http://doi.org/10.1136/bmjopen-2013-002772

White, K. R. (1982). The Relation Between Socioeconomic Status and Academic Achievement. *Psychological Bulletin*, *91*(3), 461–481. http://doi.org/10.1037/0033-2909.91.3.461

Wolf, C. (1997). The ISCO-88 International Standard Classification Of Occupations in cross-national survey research. *Bulletin de Methodologie Sociologique*, *54*(1), 23–40.

Yang, J., Benyamin, B., McEvoy, B. P., Gordon, S., Henders, A. K., Nyholt, D. R., … Visscher, P. M. (2010). Common SNPs explain a large proportion of the heritability for human height. *Nature Genetics*, *42*(7), 565–9. http://doi.org/10.1038/ng.608

Yang, J., Lee, S. H., Goddard, M. E., & Visscher, P. M. (2011). GCTA: a tool for genome-wide complex trait analysis. *American Journal of Human Genetics*, *88*, 76–82. http://doi.org/10.1016/j.ajhg.2010.11.011

Yang, J., Lee, S. H., Goddard, M. E., & Visscher, P. M. (2013). Genome-wide complex trait analysis (GCTA): Methods, data analyses, and interpretations. *Methods in Molecular Biology*, *1019*, 215–236. http://doi.org/10.1007/978-1-62703-447-0-9

Young, M. (1965). *The rise and fall of the meritocracy*. London, UK: Penguin Books.

Chapter 3: How specific is second language-learning ability? A twin study exploring the contributions of first language achievement and intelligence to second language achievement

This chapter, analysing the aetiology of second language learning, is presented as a published paper. It is an exact copy of this publication.

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Supplementary materials for this chapter, as detailed in the text, are attached in Appendix 2.

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ORIGINAL ARTICLE

How specific is second language-learning ability? A twin study exploring the contributions of first language achievement and intelligence to second language achievement

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Learning a second language is crucially important in an increasingly global society, yet surprisingly little is known about why individuals differ so substantially in second language (SL) achievement. We used the twin design to assess the nature, nurture and mediators of individual differences in SL achievement. For 6263 twin pairs, we analyzed scores from age 16 UK-wide standardized tests, the General Certificate of Secondary Education (GCSE). We estimated genetic and environmental influences on the variance of SL for specific languages, the links between SL and English and the extent to which the links between SL and English are explained by intelligence. All SL measures showed substantial heritability, although heritability was nonsignificantly lower for German (36%) than the other languages (53–62%). Multivariate genetic analyses indicated that a third of genetic influence in SL is shared with intelligence, a third with English independent of intelligence and a further third is unique to SL.

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INTRODUCTION

Learning a second language (SL) is increasingly important in modern global societies; however, surprisingly little is known about the origins of individual differences in foreign language acquisition. Given the importance of SL ability in the modern world, it is striking that only a handful of published studies have used genetically sensitive methods to investigate the etiology of individual differences in SL achievement. To our knowledge, the twin design has been applied in only three studies. A Dutch study using over 1600 12 to 26-year-old twin pairs, reported a high heritability estimate (71%).[1] However, this study used self-reported aptitude, not measured performance in SL learning. An Australian study with a relatively small sample of 251 adolescent twin pairs investigated teacher-rated achievement in SL learning and reported high heritability estimates (72%) with shared environmental factors explaining 20% of the variance.[2] The only adequately powered study using non-self-report SL measures was conducted with a subsample of the present study: teacher-rated achievement for 14-year-old twins from the Twins Early Development Study (TEDS) yielded a substantial heritability estimate of 42%, shared environmental influences of 32% and non-shared environmental influences of 26%.[3] Importantly, this study also showed shared etiology between age 12 achievement in English and SL at age 14, demonstrating substantial phenotypic (0.44) and genetic correlations (0.49) between the first and SL achievement scores. However, these results were based on teacher ratings, and, as twins often have the same teacher for a given foreign language, this measure could lead to rater bias and to an inflated estimate of shared environment. In summary, the few available studies suggest that there is substantial heritability in SL achievement; however, the results to date are mixed, as would be expected, given the diverse measures used in these studies.

It is possible that SL achievement reflects a broader language skill. Indeed, early first language skills have been shown to be closely related to achievement in SL even after a 10-year gap.[4,5] We have shown that achievement in the first language (English) is highly heritable in the early school years[6] and at the end of compulsory education.[7] In our previous report on SL, we showed that SL at the age of 14 was substantially correlated phenotypically (0.44) and genetically (0.49) with first language achievement scores.[3]

The strongest predictor of SL achievement is a construct called *second language learning aptitude*, which is generally considered as a specific ability for SL learning.[8] One way to look at this construct is in terms of ability to learn several languages; however, few students take more than one foreign language General Certificate of Secondary Education (GCSEs) and those that do are likely to be self-selected for SL-learning aptitude. SL-learning aptitude is typically measured using language-learning exercises, such as the Modern Language Aptitude Test[9] that are very similar to the actual learning outcome they are used to predict, although the underlying psychological mechanisms remain poorly understood.[10] Language-learning aptitude has been hypothesized to include memory, phonetic coding ability, language analytic ability and grammatical sensitivity,[11–13] all of which appear to be related to intelligence. For example, both language analytic ability and memory are usually considered important components of intelligence.[10] Furthermore, it is not clear whether aptitude is something different from intelligence.[14] We did not have a measure that specifically addresses SL-learning aptitude. However, in addition to investigating whether SL achievement reflects broader language aptitude that includes first language, we were able to address, for the first time, the extent to which SL achievement is even more general in the sense of general

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intelligence. Intelligence has been shown to be a significant predictor of SL achievement, as well as academic achievement in general.[15–18] In terms of genetics, intelligence, such as academic achievement, is highly heritable (~0.50).[19] For these reasons, it is important to include intelligence in a multivariate genetic investigation of SL achievement.

In summary, the current study goes beyond our previous report in three ways. First, our sample is three times larger. This increased power enabled us to investigate the main SLs studied at school separately, and also allowed for more powerful multivariate genetic analyses. Second, instead of teacher ratings, our analyses were based on standardized examinations (GCSEs) taken at the end of compulsory education in the United Kingdom. Third, we included intelligence in multivariate analyses. These measures allowed us to investigate the extent to which SL achievement reflects a broader language skill (first language achievement) and an even broader cognitive ability (intelligence). We report results for twins with GCSE scores at the age of 16 in English and SL and for whom intelligence scores were also available. We show, for the first time, the results of trivariate analyses investigating the association between intelligence, English and SL achievement.

MATERIALS AND METHODS

Sample

The sampling frame for the present study was the TEDS sample. TEDS is a large longitudinal sample involving over 16 000 twin pairs born in England and Wales during 1994–1996. Although there has been some attrition, more than 10 000 twin pairs have remained actively involved in the study. Since infancy, rich cognitive and behavioral data have been collected from the twins, including academic achievement.[20] The sample is a representative sample of the UK population when compared with data from the National Statistics Office.[6]

The present study included 12 526 individuals (6263 twin pairs) from whom GCSE scores were obtained for English or SL; intelligence scores were available for 4481 individuals (2240 pairs). The sample size for each measure is shown in the results. Children who had major medical or psychiatric problems were excluded from the analyses. Because the present study investigated achievement in first and second languages, children who did not have English as their first language were also excluded from the analyses; however, no information about the extent of bilingualism was available. Zygosity was assessed using a parent questionnaire of physical similarity, which is 95% accurate when compared with DNA testing.[21] DNA testing was conducted when zygosity was not clear from physical similarity criteria. Both same-sex twin pairs and opposite-sex twin pairs were included in the study, with the overall sample including 2229 monozygotic (MZ) pairs, 2050 same-sex dizygotic (DZ) twin pairs and 1984 opposite-sex DZ twin pairs.

Measures

We used the GCSE grades for language achievement measures at the age of 16. GCSEs are standardized examinations taken in the United Kingdom at the end of compulsory education. The GCSE courses usually begin at the age of 14 and children choose from a variety of subjects, from traditional academic subjects such as English and mathematics, to history, geography, music and foreign languages. English, mathematics and science are compulsory subjects; all other courses are chosen from a variety of available subjects. Many schools also require students to take at least one modern foreign language course. These foreign language GCSE courses include reading, writing, listening and speaking the SL; however, only one mean exam grade is awarded for each SL GCSE examination. The examinations are graded between A* and G, which we coded from 11 (A*) to 4 (G). Students typically choose 10 or more GCSEs; receiving five or more grades between A* and C (inclusive) is a requirement for further education. All GCSE scores were collected by questionnaires sent by mail or by telephone from the parents or the twins themselves. Parent- and self-reported grades for English were compared with the grades obtained from the National Pupil database for 7367 twins (NPD; https://www.gov.uk/government/uploads/system/uploads/attachment_data/file/251184/SFR40_2013_FINALv2.pdf), yielding a correlation of 0.98, which indicates high accuracy of parent- and self-reported examination scores; data were not available to make this comparison specifically for SL.

The present study used all foreign language GCSE grades available for each student to create a composite, mean SL GCSE score (2765 twin pairs). The most popular foreign languages taken at GCSE level were French (1323 twin pairs), Spanish (407 twin pairs) and German (450 twin pairs). We analyzed these three language grades separately in addition to the mean SL GCSE grade. GCSE English achievement was used as a measure of first language achievement and was computed as the mean of English language and English literature grades.

Intelligence, or general cognitive ability ('g'), was assessed from Mill Hill Vocabulary score[22] and Raven's Progressive Matrices.[23] Mill Hill vocabulary is a test of verbal ability, which consists of multiple-choice items. For each item a single word is presented at the top of the screen. Participants choose an answer that has the closest meaning to the target word. Raven's Progressive Matrices is a non-verbal ability task, consisting of a series of incomplete patterns ('matrices'). In each case, the participant is asked to identify the missing part of the pattern. These measures were obtained from the twins at the age of 16 using web-based testing. Intelligence, general cognitive ability ('g'), was indexed as the mean of the standardized verbal and non-verbal scores. Intelligence scores were available for 4481 individuals, as these data were only collected from a subsample of the TEDS twins (two out of four birth cohorts, and therefore a random subsample of participants).

Before genetic analyses, all measures were corrected for age and sex differences using regression, creating standardized residual scores. This procedure is regularly used in TEDS for analyses of twin data to avoid inflation of estimates of shared environment as members of a twin pair are otherwise identical for age and MZ twins are also identical for sex.[24] For all analyses, outliers beyond three s.d.'s from the mean were removed. Finally, all measures were transformed to the standard normal distribution using the rank-based van der Waerden transformation[25,26] to correct for the negative skew. This negative skew, demonstrating a ceiling effect, was similar to that observed in the UK population as illustrated in UK national statistics (NPD; https://www.gov.uk/government/uploads/system/uploads/attachment_data/file/251184/SFR40_2013_FINALv2.pdf).

Analyses

Descriptive statistics across sex and zygosity. The measures were described in terms of means and variance, comparing boys and girls and identical (MZ) and fraternal (DZ) twins; the mean differences for age and sex and their interaction were tested using analysis of variance (ANOVA). We have previously reported full sex-limitation genetic modeling for GCSE achievement and found little evidence for sex differences in genetic and environmental estimates.[7] We conducted similar analyses specifically for SL achievement in the present study and confirmed our previous findings suggesting significant quantitative, but no qualitative sex differences. Boys have slightly higher estimates for heritability, whereas girls have slightly higher estimates for shared environment. These differences were, however, small and had overlapping confidence intervals. For these reasons, and to increase power in the present study and to decrease the complexity of reporting, all analyses were conducted on the basis of the full sample, combining sexes and including opposite-sex pairs.

Phenotypic correlations. Phenotypic correlations were calculated between the composite GCSE SL and GCSE English, between the main GCSE SL languages of French, German and Spanish, and between SL measures and intelligence. The correlations between GCSEs in individual languages were based on a restricted sample and range, as only a minority of students took two or more GCSEs in a SL.

Twin method. The twin method was used to estimate the relative contribution of additive genetic (A), shared environmental (C) and non-shared environmental influences (E) for the variance of SL, English and intelligence measures and for the covariance between them. The twin method offers a powerful natural experiment by comparing the similarity of MZ twins to DZ twins, as MZ twins share 100% of their segregating genes, and DZ twins, just as any other siblings, share 50% of their segregating genes.[27] By comparing twin correlations for MZ and DZ twins, the relative contributions of A, C and E can be estimated. Both MZ and DZ twin pairs growing up in the same family share the same environmental influences; therefore, the correlation between twin pairs for shared environmental influences is assumed to be 1.0. Non-shared environmental influences are assumed to be unique to individuals, that is, uncorrelated between twins and not contributing to similarities between them.

Cross-twin correlations can be used to estimate ACE parameters. A is approximately double the difference between MZ and DZ correlations; C can be calculated by deducting the heritability estimate from the MZ correlations; and E can be calculated by deducting the MZ correlations from unity. E also includes measurement error.[28] These A, C and E estimates can be calculated more accurately and with confidence intervals using structural equation models with maximum likelihood estimation. We used the structural equation modeling program OpenMx.[29] Univariate parameter estimates are reported for all measures.

Bivariate genetic analysis extends univariate analysis of variance to the covariance between two variables. Similar to univariate decomposition of variance, the phenotypic covariance between traits can be decomposed into A, C and E components on the basis of cross-twin cross-trait correlations, examining the covariance between twin pairs across different traits (See Supplementary Figure S1). Genetic correlation (r_G) is an index of pleiotropy: it estimates the extent to which the same genes influence two traits independent of the heritability of the traits. By weighting the genetic correlation by the heritabilities of two traits, genetic mediation of the phenotypic correlation can be estimated. An algebraically equivalent representation of the same analysis is the Cholesky decomposition (Supplementary Figure S1b), which is conceptually similar to hierarchical regression. Cholesky decomposition focuses on the extent to which the heritability of one trait is explained by genetic influences on the other trait (path a_{12} in Supplementary Figure S1b). These analyses also decompose covariance into common shared environmental influences (r_C) and non-shared environmental influences (r_E). Two bivariate genetic analyses were conducted to assess the links between achievement in SL and achievement in first language (English), and assess the links between achievement in SL and intelligence.

Trivariate genetic analysis extends bivariate genetic analysis to consider all three variables simultaneously: intelligence, English and SL. Trivariate genetic Cholesky analysis was used to estimate (1) the extent to which the heritability of SL can be explained by genetic influence that is shared with intelligence and English, (2) how much is explained by English independent of intelligence and (3) how much genetic influence is specific to SL, independent of both intelligence and English.

RESULTS

Means and s.d.'s are presented in Table 1 by sex and zygosity for five groups: MZ males, DZ males, MZ females, DZ females and DZ opposite-sex pairs. ANOVA results show that the sex, zygosity and their interaction explain only ~1% of the variance on average.

For subsequent analyses, scores were age and sex regressed and normalized using the van der Waerden transformation, as explained in the Materials and Methods section.

Univariate model fitting

Figure 1 shows univariate ACE (additive genetic, shared environmental and non-shared environmental components of variance) estimates for the mean SL score, as well as for French, German and Spanish. SL learning at the end of compulsory education is highly heritable (56% for composite GCSE SL grade). Heritability estimates for French and Spanish are substantial, 53% and 56%, respectively. Shared environmental influence accounted for approximately a quarter (27 and 22%) of the variance. Non-shared environmental influences (*E*) that do not contribute to similarities between the twins accounted for the remaining fifth of the variance (22 and 20%). Interestingly, German language achievement at the age of 16 yields a lower heritability estimate of 36% and a higher shared environmental influence of 45%, although these estimates are not significantly different from French or Spanish. All twin correlations and detailed model-fitting results, together with confidence intervals, are presented in Supplementary Table S1.

Correlations between SL, English and intelligence

Phenotypic correlations among the three variables are substantial. English and SL correlate 0.70 (0.69–0.72: 95% confidence intervals).

Table 1. Descriptive statistics

	N	*Whole sample*	*Male*	*Female*	*MZm*	*DZm*	*MZf*	*DZf*	*DZos*	*Sex*	*Zyg*	*Sex × Zyg*	R^2
GCSE English	12 099	8.91 (1.21)	8.69 (1.26)	9.12 (1.14)	8.65 (1.27)	8.75 (1.20)	9.06 (1.13)	9.12 (1.15)	8.92 (1.23)	38.57**	3.09	0.01	0.01
GCSE SL	6896	8.82 (1.42)	8.62 (1.50)	8.96 (1.34)	8.56 (1.51)	8.70 (1.51)	8.91 (1.34)	8.98 (1.33)	8.83 (1.42)	43.45**	3.01	0.8	0.01
Intelligence	4481	0.00 (0.99)	0.05 (1.01)	−0.03 (0.98)	0.00 (0.98)	0.07 (1.05)	−0.08 (0.98)	−0.05 (1.00)	0.06 (0.99)	6.1*	6.48*	0.01	< 0.01

Abbreviations: ANOVA, analysis of variance; DZ, dizygotic; f, female; GCSE, General Certificate of Secondary Education; m, male; MZ, monozygotic; *N*, sample size after exclusions (individuals); os, opposite sex; SL, second language; Zyg, zygosity. Mean (s.d.'s) for GCSE English, GCSE SL grade, and intelligence. *Note*: The maximum GCSE grade is 11 and the minimum grade is 4, representing grades A* to G. ANOVAs were conducted by selecting randomly one twin per pair testing the main effect of sex and zygosity, and the interaction between them. Results = F statistics, R^2 = proportion of variance explained; *$P < 0.05$; **$P < 0.01$.

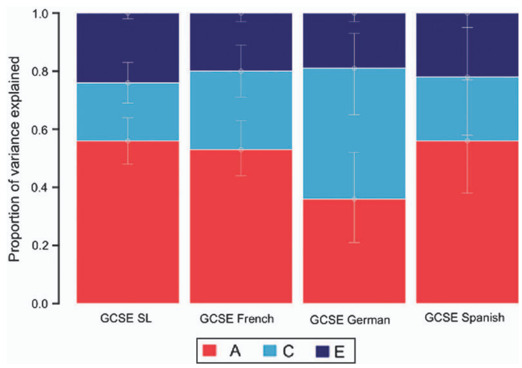

Figure 1. Univariate model-fitting results representing A, additive genetic; C, shared environmental; E, non-shared environmental components of variance for General Certificate of Secondary Education (GCSE) language measures (95% confidence interval (CI)).

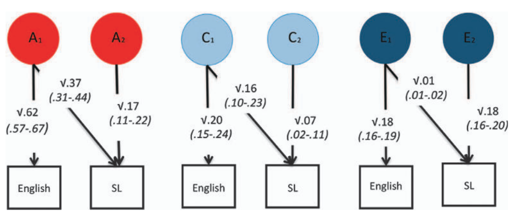

Figure 2. Bivariate model-fitting results for Cholesky decomposition for General Certificate of Secondary Education (GCSE) English and GCSE second language (SL) with 95% confidence intervals (in parentheses).

Intelligence correlates moderately with both English (0.52; 0.50–0.54) and SL (0.48; 0.45–0.51). Correlations between specific languages are also substantial (0.69–0.79), as shown in Supplementary Table S2. However, the sample size for these correlations was small and possibly not representative as it was limited to students who took more than one foreign language GCSE.

Bivariate model fitting

Figure 2 illustrates the results of bivariate genetic analyses between English and SL. The heritability of SL achievement is 54%, the sum of the two paths $\sqrt{0.37}$ and $\sqrt{0.17}$, which differs only slightly from the estimate of 56% from univariate model fitting (Supplementary Table S1). The a_{12} path (see Supplementary Figure S1) of $\sqrt{0.37}$ indicates that English accounts for 68% (0.37/0.54) of the heritability of SL at the age of 16.

Bivariate genetic analyses conducted between intelligence and SL indicate that intelligence explains 27% (0.15/0.55) of the heritability of SL achievement (see Supplementary Figure S2).

We conducted similar analyses for the specific languages of French, Spanish and German. Supplementary Figure S3 summarizes the results of these analyses. Similar to the results shown for the SL composite in Figure 2, bivariate Cholesky analyses of English as compared with the three languages showed that English accounted for ~80% of heritability of each of the languages (see Supplementary Figure S4). Similar to the results shown in Supplementary Figure S4, bivariate Cholesky analyses showed that intelligence accounted for ~30% of the heritability of each of the languages (see Supplementary Figure S5). In summary, the bivariate results shown in Figure 2 for the SL composite were similar to those that emerged for each of the languages separately; there were some differences in the magnitude of heritability explained by English, but these differences were not statistically significant. It is important to remember that we had much less power to conduct the bivariate analyses using three languages separately as compared with SL composite, as evident from the wide confidence intervals.

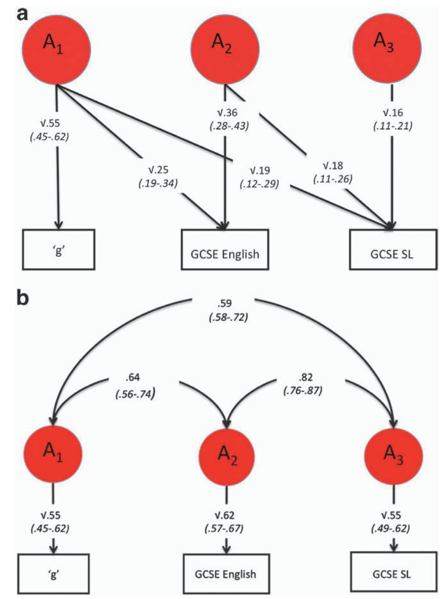

Figure 3. Trivariate genetic Cholesky analyses. (**a**) Trivariate genetic model-fitting results for Cholesky decomposition for 'g', GCSE English and GCSE SL with 95% confidence intervals (in parentheses); (**b**) correlated factor solution with 95% confidence intervals (in parentheses). GCSE, General Certificate of Secondary Education; SL, second language.

Trivariate model fitting

To investigate further the relationships between SL English and intelligence, a trivariate genetic analysis was conducted. Figure 3 presents the genetic results of (a) the Cholesky solution and (b) the correlated factor solution. The Cholesky analysis indicates that 36% (0.19/0.53) of the variance in the heritability of SL can be attributed to intelligence and English, a further 34% (0.18/0.53) of the heritability of SL can be attributed to English independent of intelligence, and 30% (0.16/0.53) of the heritability of SL is unique genetic variance, that is, independent of English and intelligence. Full Cholesky decomposition is shown in Supplementary Figure S6. The correlated factor solution (Figure 3b) yields a genetic correlation of 0.82 between SL and English, suggesting that the same genes largely contribute to these two measures. The genetic correlation between SL and intelligence is 0.59, which is significantly lower than the genetic correlation between SL and English, as seen by their nonoverlapping confidence intervals. Full correlation matrixes, together with confidence intervals, are included in Supplementary Table S3.

DISCUSSION

We found that most individual differences in SL achievement are accounted for by genetic differences, rather than school, family and other environmental influences. This conclusion holds for both Spanish and French, although there may be less genetic influence and more shared environmental influence for German.

These heritability estimates are higher than those in our earlier study,[3] which might be because different measures were used. In the present study we used standardized examination scores at the end of compulsory education, as compared with teacher ratings of academic achievement in our earlier report. Secondly, the teacher-rated measure used previously was collected at the age of 14, which is typically in the middle of SL learning. Our current measure was obtained at the end of formal SL education, when individual differences may have become more stabilized.

Our bivariate results demonstrate a general genetic factor of language achievement at the end of compulsory education in the United Kingdom in the sense that achievement in English and SL is influenced to a large extent by the same genes. Furthermore, genetic influence on SL achievement cannot be explained by intelligence alone. SL heritability is just as much explained by English achievement as it is by intelligence, and the genetic bivariate relationship between SL and English is stronger than the bivariate genetic relationship between SL and intelligence. A more comprehensive picture is provided by our trivariate results, which show that genetic influences on intelligence contribute about one-third of the heritability of SL achievement. A further third of the heritability of SL can be accounted for by genetic influence on English independent of intelligence, pointing to a general factor of language. The final third of the heritability of SL is unique to SL, that is, independent of both intelligence and English.

We believe our study is the first adequately powered study to employ standardized examination results for SL learning at the end of compulsory education in order to estimate genetic and environmental influences on the variance and covariance of first and SL achievement and intelligence. There are, however, at least four limitations that need to be acknowledged. First, the usual assumptions about twin method were made, which are described in detail elsewhere.[27] Second, the instructed language learning studied here could differ from learning in a natural setting, and therefore the results of this study cannot be generalized to SL acquisition outside of classroom settings,[30,31] and only apply to those who have chosen to take GCSE in SL. Third, some schools in the United Kingdom require students to take at least one foreign language GCSE, whereas others do not allow pupils to choose more than one; therefore, we could not investigate the genetic and environmental origins of individual differences in choosing one or more foreign language GCSE courses. Furthermore, because SL GCSE is compulsory in some schools but not in other schools, it might not be a random group of students who took one or more foreign language GCSE courses. Finally, the foreign language GCSE examination consists of four parts: reading, writing, listening and speaking, which make it a reliable measure of overall academic achievement in language learning. However, only one composite grade per language is awarded at GCSE level, so that we could not distinguish these different aspects of language learning as they relate to English achievement or intelligence. We created the composite of English language and English literature because there is substantial overlap with the course content measuring reading, writing, speaking and listening skills. Nonetheless, we checked whether analyzing the English language grade by itself yields similar results; the results are highly similar to those shown for the composite measure. It is also noteworthy that both GCSE English and GCSE SL are assessed by standardized examinations, whereas intelligence is not. Thus, it is possible that shared method variance contributes to the correlation between English and SL.

The present results suggest several questions for further research on academic achievement in SLs. Our future research involves longitudinal investigations into SL achievement, for example, a longitudinal analysis exploring how early English achievement and intelligence relate etiologically to SL at the age of 16. We will also explore whether the conclusions presented here for the entire sample hold at the extremes of exceptionally high or low SL achievement. If appropriate samples can be found, multivariate genetic analyses should be conducted in different foreign languages to investigate the extent to which the same genetic and environmental factors influence learning diverse foreign languages. This was not possible in the present study because few students took more than one foreign language GCSE. Furthermore, all of the students in this study were native speakers of English. It would be of considerable theoretical interest to explore the role of first and SL typological distance as an influence on SL etiology, that is, how the differences between languages on various aspects of linguistic structure influence the rate of language learning and achievement. A large body of literature has shown that SL-learning aptitude, learning styles and quality of instruction are significant predictors of the rate of SL learning.[12,32–34] Further research is needed to study the etiology of the associations between these predictors and achievement in SL using a multivariate genetic design, and this is one of our goals for future research. Another goal is to understand the role of specific cognitive abilities, not just general intelligence, on SL achievement. One strategy that could prove useful in this regard is to study individuals with discrepancies between GCSE grades in English and SL.

We have demonstrated here that genes explain a larger proportion of differences between children in SL achievement than do shared environmental influences of school and home environment. It is important to note that genes not only influence the aptitude and achievement of children directly, but also their appetite for knowledge and hence indirectly their eventual achievement. This is an example of genotype–environment correlation; as children grow older they tend to select, modify and tailor their environment on the basis of their genetic propensities.[35] Genotype–environment correlation may be increasingly important during adolescent development; achievement in language learning could be influenced by how much students use the language outside the school, their interest in the different cultures and self-efficacy.

Achievement at the end of compulsory education is of major, and increasing, importance to society and to individuals because these results are used to make decisions regarding further education and occupation. The findings of our study will become even more important once specific genes responsible for academic achievement in SL learning are identified, unique environmental factors are ascertained and gene–environment interplay is better understood.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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DISCLAIMER

The funders had no role in study design, data collection and analysis, decision to publish or preparation of the manuscript.

REFERENCES

1 Vinkhuyzen AAE, van der Sluis S, Posthuma D, Boomsma DI. The heritability of aptitude and exceptional talent across different domains in adolescents and young adults. *Behav Genet* 2009; **39**: 380–392.
2 Coventry W, Antón-Méndez I, Ellis EM, Levisen C, Byrne B, van Daal VHP *et al.* The etiology of individual differences in second language acquisition in Australian school students: a behavior-genetic study. *Lang Learn* 2012; **62**: 880–901.
3 Dale PS, Harlaar N, Plomin R. Nature and nurture in school-based second language achievement. *Lang Learn* 2012; **62**: 28–48.
4 Melby-Lervåg M, Lervåg A. Cross-linguistic transfer of oral language, decoding, phonological awareness and reading comprehension: a meta-analysis of the correlational evidence. *J Res Read* 2011; **34**: 114–135.
5 Sparks R, Patton J, Ganschow L, Humbach N. Long-term crosslinguistic transfer of skills from l1 to l2. *Lang Learn* 2009; **59**: 203–243.
6 Kovas Y, Haworth CMA, Dale PS, Plomin R. The genetic and environmental origins of learning abilities and disabilities in the early school years. *Monogr Soc Res Child Dev* 2007; **72**: 1–144.
7 Shakeshaft NG, Trzaskowski M, McMillan A, Rimfeld K, Krapohl E, Haworth CMA *et al.* Strong genetic influence on a UK nationwide test of educational achievement at the end of compulsory education at age 16. *PLoS ONE* 2013; **8**: e80341.
8 Dörnyei Z, Skehan P. Individual differences in second language learning. In: Doughty CJ, Long MH (eds). *The Handbook of Second Language Acquisition*. Wiley-Blackwell, 2005, p 589.
9 Carroll J, Sapon SM. *Modern Language Aptitude Test*. Psychological Corporation: New York, NY, USA, 1959.
10 DeKeyser R, Koeth J. Cognitive aptitudes for second language learning. In: Hinker L (ed). *Handbook of Research in Second Language Teaching and Learning,* Vol. 2. Routledge: New York, NY, USA, 2011, pp 395–406.
11 Carroll JB. The prediction of success in intensive foreign language training. In: Glaser R (ed). *Training research and education*. University of Pittsburgh Press: Pittsburgh, pp 87–136, 1962.
12 Dörnyei Z. Individual differences in second language acquisition. *AILA Rev* 2006; **19**: 42–68.
13 Skehan P. *A Cognitive Approach to Language Learning*. Oxford University Press: Oxford, UK, 1998.
14 Teepen J. On the relationship between aptitude and intelligence in second language acquisition. *Teach Coll Columbia Univ Work Pap TESOL Appl Linguist* 2005; **4**: 1–9.
15 Deary IJ, Strand S, Smith P, Fernandes C. Intelligence and educational achievement. *Intelligence* 2007; **35**: 13–21.
16 Gardner RC. Second-language learning in adults: correlates of proficiency. *Appl Lang Learn* 1991; **2**: 1–28.
17 Linck JA, Osthus P, Koeth JT, Bunting MF. Working memory and second language comprehension and production: a meta-analysis. *Psychon Bull Rev* 2014; **21**: 861–883.
18 Pishghadam R, Khajavy GH. Intelligence and metacognition as predictors of foreign language achievement: a structural equation modeling approach. *Learn Individ Differ* 2013; **24**: 176–181.
19 Deary IJ, Johnson W, Houlihan LM. Genetic foundations of human intelligence. *Hum Genet* 2009; **126**: 215–232.
20 Haworth CMA, Davis OSP, Plomin R. Twins Early Development Study (TEDS): a genetically sensitive investigation of cognitive and behavioral development from childhood to young adulthood. *Twin Res Hum Genet* 2013; **16**: 117–125.
21 Price TS, Freeman B, Craig I, Petrill SA, Ebersole L, Plomin R. Infant zygosity can be assigned by parental report questionnaire data. *Twin Res* 2000; **3**: 129–133.
22 Raven J, Raven JC, Court J. *Manual for Raven's Progressive Matrices and Vocabulary Scales*. Oxford University Press: Oxford, 1996.
23 Raven JC, Raven J, Court JH. *The Mill Hill Vocabulary Scale*. OPP: Oxford, UK, 1998.
24 McGue M, Bouchard TJ. Adjustment of twin data for the effects of age and sex. *Behav Genet* 1984; **14**: 325–343.
25 Lehmann E. *Nonparametric Statistical Methods Based on Ranks*. Holden-Day: San Francisco, CA, USA, 1975.
26 Van Der Waerden BL. On the sources of my book Moderne Algebra. *Hist Math* 1975; **2**: 31–40.
27 Plomin R, DeFries JC, Knopik VS, Neiderhiser JM. *Behavioral Genetics*. 6th edn, Worth Publishers: New York, NY, USA, 2013.
28 Rijsdijk FV, Sham PC. Analytic approaches to twin data using structural equation models. *Brief Bioinform* 2002; **3**: 119–133.
29 Boker S, Neale M, Maes H, Wilde M, Spiegel M, Brick T *et al.* OpenMx: an open source extended structural equation modeling framework. *Psychometrika* 2011; **76**: 306–317.
30 Ellis R. *Second Language Acquisition*. Oxford: Oxford University Press, 1997.
31 Ellis R. Understanding second language acquisition. *The Oxford Applied Linguistics.* OUP Oxford, 1985.
32 Ehrman ME, Leaver B Lou, Oxford RL. A brief overview of individual differences in second language learning. *System* 2003; **31**: 313–330.
33 Lyster R, Saito K, Sato M. Oral corrective feedback in second language classrooms. *Lang Teach* 2012; **46**: 1–40.
34 Lyster R, Saito K. Oral feedback in classroom SLA. *Stud Second Lang Acquis* 2010; **32**: 265–302.
35 Asbury K, Plomin R. *G is for Genes: The Impact of Genetics on Education and Achievement*. John Wiley & Sons, 2013.

Supplementary Information accompanies the paper on the Translational Psychiatry website (http://www.nature.com/tp)

Chapter 4: The high heritability of educational achievement reflects many genetically influenced traits, not just intelligence

This chapter, analysing the aetiology of academic achievement at the end of compulsory education, is presented as a published paper. It is an exact copy of this publication.

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Supplementary materials for this chapter, as detailed in the text, are attached in Appendix 3.

The high heritability of educational achievement reflects many genetically influenced traits, not just intelligence

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Because educational achievement at the end of compulsory schooling represents a major tipping point in life, understanding its causes and correlates is important for individual children, their families, and society. Here we identify the general ingredients of educational achievement using a multivariate design that goes beyond intelligence to consider a wide range of predictors, such as self-efficacy, personality, and behavior problems, to assess their independent and joint contributions to educational achievement. We use a genetically sensitive design to address the question of why educational achievement is so highly heritable. We focus on the results of a United Kingdom-wide examination, the General Certificate of Secondary Education (GCSE), which is administered at the end of compulsory education at age 16. GCSE scores were obtained for 13,306 twins at age 16, whom we also assessed contemporaneously on 83 scales that were condensed to nine broad psychological domains, including intelligence, self-efficacy, personality, well-being, and behavior problems. The mean of GCSE core subjects (English, mathematics, science) is more heritable (62%) than the nine predictor domains (35–58%). Each of the domains correlates significantly with GCSE results, and these correlations are largely mediated genetically. The main finding is that, although intelligence accounts for more of the heritability of GCSE than any other single domain, the other domains collectively account for about as much GCSE heritability as intelligence. Together with intelligence, these domains account for 75% of the heritability of GCSE. We conclude that the high heritability of educational achievement reflects many genetically influenced traits, not just intelligence.

academic achievement | twin studies | behavioral genetics | general cognitive ability | personalized learning

Education is one of society's biggest and most expensive environmental interventions in children's development, accounting for more than 6% of the gross domestic product in many countries (1). Differences among children in their educational achievement, especially culminating at the end of compulsory schooling, propel children on different lifelong pathways that affect higher education, occupation, and even health and mortality (1–4). Not only are differences in educational achievement important to society and to children as individuals, they are also a focal concern for parents (5, 6). For these reasons, it is important to understand the causes and correlates of differences among children in their educational achievement.

Educational achievement refers to mastery of specific content, including knowledge and skills for subjects such as literacy, numeracy, and science. The word achievement, in contrast to ability, connotes accomplishments by dint of effort. It is often assumed that effort is relatively more environmentally influenced than ability and thus that differences between children in their educational achievement are environmental in origin, reflecting differences among classrooms, schools, and parents (7, 8). This assumption is reasonable because, for example, most children will not learn to read or do arithmetic unless they are taught. However, genetic research has shown that individual differences in educational achievement are substantially heritable (9–11). Indeed, we have shown that educational achievement is significantly more heritable than intelligence in the early school years (12). We have recently found high heritability (58%) for the results of a nationwide examination, the General Certificate of Secondary Education (GCSE), which is administered in the United Kingdom at the end of compulsory education at age 16 (13).

The present study asks why individual differences in educational achievement at the end of compulsory education are so highly heritable, focusing on children's characteristics. Most phenotypic studies of the correlates of educational achievement have investigated intelligence or working memory (14–16). Correlations between IQ and educational achievement range between 0.4 and 0.7 (17). However, dozens of other traits have also been shown to relate to educational achievement, such as self-efficacy and motivation (18–21), emotional intelligence (22–25), personality (26–29),

Significance

Differences among children in educational achievement are highly heritable from the early school years until the end of compulsory education at age 16, when UK students are assessed nationwide with standard achievement tests [General Certificate of Secondary Education (GCSE)]. Genetic research has shown that intelligence makes a major contribution to the heritability of educational achievement. However, we show that other broad domains of behavior such as personality and psychopathology also account for genetic influence on GCSE scores beyond that predicted by intelligence. Together with intelligence, these domains account for 75% of the heritability of GCSE scores. These results underline the importance of genetics in educational achievement and its correlates. The results also support the trend in education toward personalized learning.

Author contributions: E.K., K.R., P.S.D., and R.P. designed research; E.K., K.R., and A.M. contributed new reagents/analytic tools; E.K., K.R., N.G.S., M.T., and A.M. analyzed data; and E.K., K.R., N.G.S., M.T., A.M., J.-B.P., K.A., N.H., Y.K., P.S.D., and R.P. wrote the paper.

The authors declare no conflict of interest.

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prosocial behavior (5), well-being (30), goals (31), curiosity (32), beliefs about intelligence (33), self-efficacy (34), behavior problems (35, 36), health (37), and children's perceptions of their home environment (38) and their school environment (39). These traits are intercorrelated, which suggests the need for multivariate studies that can consider their joint and separate contributions to educational achievement. However, few broad multivariate phenotypic studies have been reported, although several studies have included intelligence in addition to another variable in predicting educational achievement (28, 40, 41). Recently, a theoretical model that attempted to integrate research on predictors of educational achievement focused on intelligence, specific interests, and personality, especially intellectual curiosity and conscientiousness (42).

Phenotypic correlations between such traits and educational achievement can be mediated genetically or environmentally, which is important because environmentally driven associations may be better targets for intervention. Relatively few studies have used genetically sensitive designs that can disentangle genetic and environmental sources of phenotypic correlations between children's traits and their educational achievement. Genetically sensitive studies have largely focused on intelligence, consistently showing that the phenotypic correlation between intelligence and educational achievement is mediated genetically to a substantial extent (43–50). Only a handful of studies have considered genetic contributions to educational achievement from other traits in addition to intelligence, such as self-efficacy (51), motivation (52, 53), personality (54), behavior problems (55–58), and perceptions of home environment (59) and school environment (60). Because these behavioral traits are correlated with each other and with educational achievement, adding up their separate genetic contributions to educational achievement could exceed the heritability of educational achievement. Multivariate genetic research is needed that considers the joint and independent contributions of a wide range of predictors to the heritability of educational achievement, taking into account the intercorrelations among the predictors. The only example to date is a twin study of longitudinal stability of teachers' grades at ages 11–17 for 800 pairs of twins that also reported multivariate genetic analyses, in which the heritability of teachers' grades at age 11 were largely explained collectively by genetic factors involved in intelligence, engagement, and externalizing behavior problems (61). This report led us to hypothesize that the substantial heritability of test scores at the end of compulsory education could almost entirely be explained by a larger set of predictors that includes self-efficacy, personality, and well-being.

The Current Study

We included diverse behavioral correlates of educational achievement in a multivariate genetic design, which allowed us to consider the joint and separate contributions of these traits to the heritability of educational achievement, taking into account the intercorrelations among the traits. Our study was sufficiently large to achieve adequate power to discriminate genetic and environmental estimates of variance and covariance between these behavioral correlates and educational achievement. The sample was from the UK Twins Early Development Study (62) and included 6,653 pairs of twins assessed on a set of examinations of educational achievement, called the GCSE, administered nationwide under standardized conditions at the end of compulsory education, typically at age 16. We created a composite GCSE score based on the three compulsory core subjects of English, mathematics, and science, which correlated 0.70 on average (see *Methods* for details about the sample and measures).

We focused on nine broad domains of candidate correlates of educational achievement: intelligence, self-efficacy, personality, well-being, parent-rated behavior problems, child-rated behavior problems, health, perceived school environment, and perceived home environment. Each domain is represented by a general composite rather than analyzing each of the scales within each domain. The reason for using composite indices is that they make the multivariate genetic analyses manageable and they provide an overview of the extent to which these diverse domains of behavior—considered separately and jointly—explain the heritability of educational achievement. In addition, our study was limited to measures included in the assessment of 16-y-old twins in the Twins Early Development Study (TEDS). Although the TEDS assessment was extensive, including 83 scales, it did not include all of the dozens of variables that have been reported to be associated with educational achievement. These two limitations—the use of general composite indices and the noninclusion of some measures—are conservative in the sense that including more fine-grained measures and additional variables might explain even more of the heritability of educational achievement. Conversely, if, as we hypothesized, most of the heritability of educational achievement is accounted for by these composite indices, this suggests that other predictors do not make a major independent contribution to the heritability of educational achievement after accounting for the predictors in the current study.

Results

The twin method was used to conduct univariate, bivariate, and multivariate analyses of genetic and environmental influences on the variance and covariance of the GCSE core subjects composite (henceforth just GCSE) and its correlates (see *Methods* for a description of the twin method and analyses). Table S1 shows means and SDs for the unadjusted GCSE core measure by the five twin groups arising from sex and zygosity. The observed mean sex differences are very small [males 8.86 (1.23), females 8.96 (1.21)]; the difference is statistically significant because of the very large sample size. Sex, zygosity, and their interaction account for less than 1% of the variance, and for subsequent analyses, after outliers were removed, variables were age and sex regressed and normalized using van der Waerden transformation as explained in *Methods.* Full sex limitation genetic modeling has previously been reported for GCSE and found only very minor sex differences in genetic and environmental estimates (13). In addition, the only other multivariate genetic analysis of this type found little evidence of sex differences (61). For these reasons and to increase power, the present analyses are based on the total sample, combining sexes.

Univariate Genetic Analyses. GCSE is more highly heritable (62%) than any of the nine predictor variables (35–58%), as summarized in Fig. 1. Shared environmental influence, which could be due to shared family or school environments, accounted for about a quarter of the variance of GCSE (26%) and were 0% for

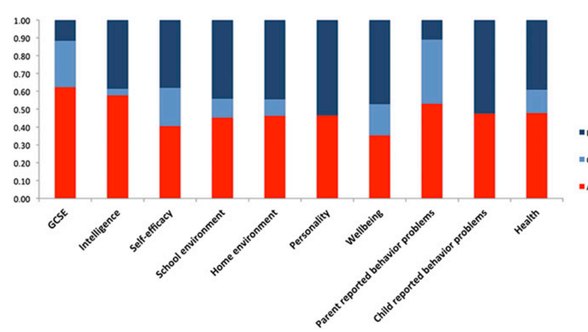

Fig. 1. Model fitting results for additive genetic (A), shared environment (C), and nonshared environment (E) components of variance for GCSE and nine predictors.

personality and child-rated behavior problems, 4% for intelligence, 21% for self-efficacy, and 36% for parent-rated behavior problems. Twin correlations are shown in Table S2 and model-fitting univariate estimates are presented in Table S3 for the standard ACE model that estimates additive genetic (A), shared environmental (C), and nonshared environmental (E) components of variance.

Bivariate Genetic Analyses. Fig. 2 illustrates the results of bivariate genetic analyses, which estimate the extent to which the phenotypic correlations between GCSE and each of the nine domains are mediated by genetic and environmental influences. The total length of the bar represents the phenotypic correlation between each of the domains and GCSE. The highest correlations with GCSE emerged for intelligence (0.58), self-efficacy (0.49), parent-rated behavior problems (0.33), and perceptions of school environment (0.34). The full correlation matrix is presented in Table S4.

Fig. 2 shows the proportion of the phenotypic correlation between GCSE and each domain that is explained by genetic, shared environmental, and nonshared environmental influences. For most of these domains, genetic influences in common with GCSE accounted for more than half of their correlation: intelligence (75%), self-efficacy (64%), perceptions of school environment (59%), personality (92%), well-being (53%), and behavior problems (81% for parent-rated, 89% for child-rated). Shared environment significantly mediated the phenotypic correlation with GCSE for intelligence (15%), self-efficacy (21%), school environment (31%), home environment (81%), well-being (34%), and health (28%). Cross-twin cross-trait correlations are shown in Table S2, and model-fitting estimates are included in Table S5.

Fig. 3 reorganizes the nine bivariate genetic analyses using Cholesky analysis (*Methods*) to show the extent to which the heritability of GCSE can be attributed to each predictor, in nine separate bivariate analyses. The length of the bar indicates the heritability of GCSE, which is estimated at 63% on average across the nine bivariate genetic analyses. The Cholesky analysis divides the heritability of GCSE into variance attributed to the predictor variable and residual variance, which indicates genetic influences on individual differences in GCSE independent of the predictor. The greatest contributions to GCSE heritability are from intelligence (51%) and self-efficacy (37%), with additional contributions from child-rated school environment (20%), personality (21%), well-being (8%), and behavior problems, both parent-rated (21%) and child-rated (16%). Child-rated health and home environment do not contribute to the heritability of GCSE. Model-fitting estimates for Fig. 3 are included in Table S6.

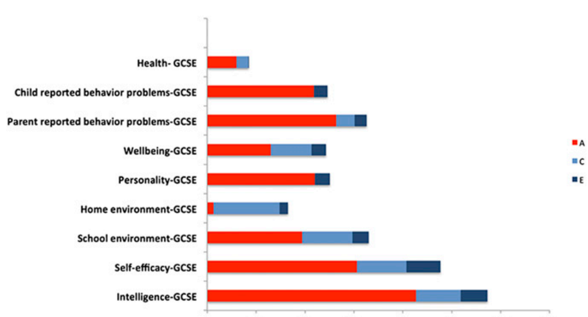

Fig. 2. Bivariate estimates for additive genetic (A), shared environmental (C), and nonshared environmental (E) contributions to the correlations between GCSE and nine predictors. The total length of the bar indicates the phenotypic correlations.

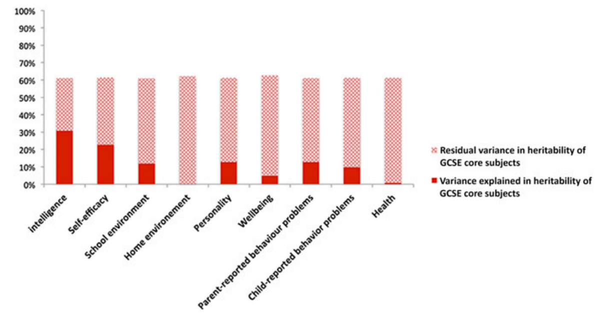

Fig. 3. Bivariate estimates of the extent to which the heritability of GCSE can be accounted for by each of the nine predictors, respectively (path a_{12} from the Cholesky decomposition; Fig. S1).

Multivariate Genetic Analyses. In summary, although intelligence accounts for most GCSE heritability, other domains also contribute significantly to GCSE heritability. Because the predictor variables correlate with each other (e.g., intelligence and self-efficacy correlate 0.35; see Table S4 for the full correlation matrix), their contributions to GCSE heritability exceed 100% when summed across the nine separate bivariate genetic analyses. For this reason, we conducted a multivariate genetic analysis including all nine predictors simultaneously to estimate how much of the GCSE variance they explain jointly. Phenotypically, in a multivariate Cholesky (conceptually similar to multiple regression) of GCSE on the nine predictors, the nine predictors account for 45% of the variance of GCSE. Multivariate genetic analysis (Cholesky) revealed that 75% of the heritability of GCSE is explained jointly by the nine predictors. Table S7 provides details of the results of the phenotypic and genetic multivariate analyses, and Tables S8–S10 provide details for genetic, shared environmental, and nonshared environmental correlation matrices.

We conducted an additional multivariate genetic analysis that asked whether, independent of intelligence, the other predictors collectively account for GCSE heritability. The eight predictors other than intelligence explain 50% of the GCSE heritability; adding intelligence raised this to 75%. Conversely, intelligence by itself explains 51% of GCSE heritability (Fig. 3 and Table S7).

Discussion

We found that, although intelligence accounts for more of the heritability of educational achievement at age 16 than any of the other domains, the other domains collectively accounted for about as much GCSE heritability as intelligence. Collectively, all cognitive and noncognitive predictors accounted for 75% of the heritability of GCSE. These genetic results turn some fundamental assumptions about education upside down. For example, one of the reasons that the contribution of intelligence is sometimes considered controversial when discussing educational outcomes is that intelligence is viewed as genetic, whereas achievement is thought to be due to environmentally driven influences from home and school. In addition, other behavioral traits such as self-efficacy are presumed to contribute to educational achievement for environmental reasons. However, our results suggest the opposite: Genetic influence is greater for achievement than for intelligence, and other behavioral traits are related to educational achievement largely for genetic reasons.

Although correlates of educational achievement have been the target of much research, there have been few multivariate studies, especially using genetically sensitive designs. With nine broad cognitive and noncognitive domains of children's behavior distilled from 83 scales, our phenotypic results show that educational achievement is correlated with many characteristics of children, not just intelligence. Our bivariate genetic results indicate that these phenotypic correlations are largely mediated by genetic factors. That is, to the extent that children's traits predict educational achievement, they do so largely for genetic reasons, for example, for personality (92%), behavior problems (81% for parent-rated, 89% for child-rated), intelligence (75%), self-efficacy (64%), and well-being (53%). Although intelligence accounts for more GCSE heritability than any other single domain, almost as much of the genetic contribution to GCSE heritability comes from the joint contribution of children's self-efficacy, behavior problems, personality, well-being, and their perceptions of school environment. In our multivariate genetic analyses across the nine domains, we were able to account for 75% of the high heritability (62%) of differences between children in their educational achievement at the end of compulsory schooling on the United Kingdom-wide GCSE examinations. The only previous relevant study was primarily a longitudinal genetic analysis of teachers' grades in a sample one-sixth the size of the present study (61). Although not the focus of that study, it included multivariate genetic results for teachers' grades at age 11 that were similar to those presented here for test scores at the end of compulsory education at age 16. What these findings mean is that children differ for genetic reasons in how easily they learn and perform at the examinations, and not just because of differences in intelligence, but because of a whole package of genetically related characteristics including self-efficacy, personality, and behavior problems, as well as intelligence.

In this study, our goal was to describe the general genetic landscape of educational achievement using broad behavioral domains. The next step in this program of research is to zoom in for more fine-grained analyses within each domain, both phenotypically and especially genetically, which is the unique contribution of our large twin study. For example, within the domain of intelligence, what are the relative contributions of verbal and nonverbal abilities to GCSE heritability? Within personality, what are the relative contributions of the general "Big Five" personality traits such as extraversion and neuroticism, as well as traits more specific to educational achievement such as grit, confidence, and optimism? For behavior problems, phenotypic research suggests, for example, that inattention symptoms are more predictive of educational outcomes than hyperactivity symptoms (36), and genetic research suggests that externalizing problems such as inattention are more predictive than internalizing problems such as depression (61).

Although we focused on the genetic findings from this study to address the question of why educational achievement is so highly heritable, the results are also instructive about environmental influences, which can only be disentangled from genetic influences in genetically sensitive designs such as the twin method. Most notably, shared environmental influence, which could be due to the effects of shared family environment or shared schools, accounts for 26% of the variance of educational achievement. This shared environmental estimate could also be partially due to assortative mating, as educational achievement and intelligence have been reported to be subject to assortative mating where mate selection depends on trait similarity between spouses (63). However, if the sources of the variance are indeed shared environmental factors, a question for future research is the source of this influence that accounts for a quarter of the variance in GCSE test scores and would appear to be an especially good target for intervention. At first glance, from our results, family and school environment are both important candidates to explain shared environmental influences on GCSE. More fine-grained studies will be needed to identify precise environmental predictors.

It is important to emphasize that finding genetic influence is not a counsel of despair in terms of helping children who find learning difficult—heritability does not imply immutability. Heritability describes the extent to which phenotypic variance can be ascribed to DNA differences, on average, in a particular population at a particular time. In other words, heritability describes what is; it does not predict what could be. For example, despite high heritability, with sufficient educational effort, nearly all children could reach minimal levels of literacy and numeracy, which is an explicit goal of education in Finland (64). Success in achieving that goal would reduce phenotypic variance, which could change heritability. Another example is greater equality of opportunity in education would decrease environmental sources of variance and thus increase heritability, which has been demonstrated empirically (65). Nonetheless, our results are important for education in pointing to the pervasive role of genetics and not just for educational achievement itself, nor just for intelligence, but also for most of the other correlates of educational achievement. The ubiquitous impact of genetics in education suggests the need for a new model for education that moves from a passive model of schooling as instruction (instruere, meaning "to build in") to an active model of education (educare, meaning "to bring out") (7). That is, education is more than what happens to a child passively; children are active participants in selecting, modifying, and creating their experiences that are correlated with their genetic propensities, known in genetics as genotype–environment correlation.

No policy implications necessarily follow from finding that genetics permeates educational achievement, because policy depends on values and knowledge. However, it is to be hoped that better policy decisions can be made with knowledge of genetic influence rather than assuming that all differences are environmental in origin (7). For example, it is worth knowing that the successful realization of values such as equality of educational opportunity will not get rid of genetic differences between children. To the contrary, heritability is likely to increase as environmental differences such as educational inequalities are removed; in this sense, heritability can be considered as an index of equality. Philosophically, it is important to recognize that children differ for genetic reasons in how easy and enjoyable they find learning. For example, genetic thinking counters the deplorable tendency to blame teachers and parents rather than recognizing that learning is inherently more difficult for some children and that differences in children's educational achievement are more a matter of genes than schools or home environments. At the practical level of curricula, the active genotype–environment correlation model of education adds support for the trend in education toward personalized learning. This trend toward personalized learning has become more practical with rapid advances in technology and educational software to supplement or supplant one-size-fits-all traditional systems of education. More specifically, our results showing strong connections between noncognitive domains and educational achievement suggest that these domains are also plausible candidates for intervention, although there is a need for longitudinal research such as cross-lagged analysis to explore causality more explicitly.

Methods

Participants. TEDS is a multivariate longitudinal study that recruited more than 11,000 twin pairs born in England and Wales in 1994, 1995, and 1996. The recruitment process and the sample are described in detail elsewhere (62). The TEDS sample is representative of the UK population compared with the data obtained by the Office of National Statistics (46). The project received approval from the King's College London Institute of Psychiatry ethics committee, and parental consent was obtained before data collection.

The sample for the present study included all individuals who had GCSE and other measures available at the age of 16. GCSE results at age 16 were available for 13,306 individuals. Children with major medical or psychiatric problems or severe perinatal medical problems were excluded from the analyses. Additionally, children whose first language was not English and whose zygosity was unknown or uncertain were excluded. Zygosity was assessed through a parent questionnaire of physical similarity, shown to be 95% accurate when validated against DNA testing (66). DNA testing was conducted where zygosity was unclear from this questionnaire. The present analyses were thus conducted on 13,306 individuals comprising 6,653 twin pairs: 2,362 monozygotic (MZ) pairs, 2,155 same-sex dizygotic (DZ) twin pairs, and 2,136 opposite-sex DZ twin pairs.

GCSE Measures. The GCSE is a UK nationwide examination taken at the end of the compulsory education. GCSE courses start typically at the age of 14, and the examinations are taken at the age of 16. The courses include a variety of subjects from traditional core academic subjects such as English and mathematics, to geography, history, music, modern foreign languages, physical education, and information and communication technology (ICT). Typically, students take 10 or more GCSE examinations at the end of compulsory education. English, mathematics, and science (composed of single-weighted or double-weighted science, or when taken separately, physics, chemistry, and biology) are compulsory courses. Many schools also require students to take English literature and one modern foreign language. The data for the present study were collected by questionnaires sent by mail and by telephone interview of parents and twins themselves. After completed forms were received from the families, the grades were coded from 11 (the highest grade, A*) to 4 (the lowest pass grade, G); no information about failed results was available. For 7,367 twins, self- and parent-reported GCSE results were verified using data obtained from the National Pupil database (NPD; www.gov.uk/government/uploads/system/uploads/attachment_data/file/251184/SFR40_2013_FINALv2.pdf), yielding correlations of 0.98 for English, 0.99 for mathematics, and >0.95 for all sciences.

For the present study, a composite measure of the compulsory core subjects was calculated and used in all analyses, because the scores on the core subjects were highly correlated (average of 0.70). This GCSE core measure was constructed as the mean of English, mathematics, and science scores: the mean of the English grade (the English language grade, or the mean of the English language grade and the English literature grade if both were taken), the science mean composite (the mean of all science GCSEs taken), and the mathematics grade. A GCSE core composite was created only if at least two of the three measures were available.

The GCSE measure was corrected for the small mean effects of age and sex (Table S1) by rescoring the variable as a standardized residual correcting for age and sex, as is standard practice in the analysis of twin data because members of a twin pair are identical in age and MZ twins are identical for sex, which would otherwise inflate twin estimates of shared environment (67). Finally, before conducting twin analyses, the GCSE measure was corrected for skew because the measure was negatively skewed, showing a ceiling effect similar to that observed in UK national statistics (NPD; www.gov.uk/government/uploads/system/uploads/attachment_data/file/251184/SFR40_2013_FINALv2.pdf). The GCSE measure was corrected for skew by mapping it on to a standard normal distribution using the rank-based van der Waerden's transformation (68, 69).

Measures Used to Predict GCSE. Data obtained from the twins and their families at age 16 for a range of cognitive and noncognitive measures were used to predict GCSE scores. These 83 measures were reduced to nine domains for the purpose of data reduction only; it should be noted that each domain was not assumed to reflect a single underlying latent factor. The data were collected by web-testing and questionnaires sent by mail.

Before domain composites were created, scales that correlated negatively with GCSE (such as behavior problems) were reversed so that scales within each domain could be summed and averaged. As with GCSE, all 83 scales were rescored as standardized residuals correcting for mean effects of age and sex. The scales were standardized with a mean of 0 and a SD of 1.0 so that they contributed equally when summed and averaged for each domain. Mean scores were calculated in this way for nine domains: general intelligence (Raven's Progressive Matrices and Mill Hill Vocabulary test), educational self-efficacy (5 scales such as academic self-concept, interest/enjoyment, attitudes toward key subjects), child-reported personality (10 scales such as Big Five Factors, optimism, and grit), child-reported well-being (17 scales, such as life satisfaction, happiness, hopefulness), parent-reported behavioral problems (12 scales such as hyperactivity, impulsivity, emotional lability), child-reported behavioral problems (8 scales such as peer problems, antisocial behavior, depression), child-reported health (9 scales such as body mass index, puberty status, sleep problems), child-reported school environment (10 scales such as engagement with school, attitudes to school, classroom environment), and child-reported home environment (10 scales such as chaos, monitoring, support). A more detailed description of the scales used to create composites is available at www.teds.ac.uk/downloads/Description83scales9domains.pdf. Composite scores were coded as missing when more than 40% of scales within that domain were missing.

Analyses. The twin method was used to conduct univariate, bivariate, and multivariate analyses of genetic and environmental influences on the variance and covariance of GCSE and the predictors of GCSE. The twin method assumes that twins reared together resemble each other due to the additive effects of shared genes or shared environmental factors. Identical, or MZ, twins share all segregating genes and are therefore 100% similar genetically. Nonidentical, or DZ, twins, on average, share half their segregating alleles, resulting in 50% genetic resemblance (like nontwin siblings). The correlation between twins for shared environmental effects is assumed to be 1.0 for both MZ and DZ twins growing up in the same family. Nonshared environmental influences are uncorrelated between twins and contribute to differences between them. On this basis, it is possible to decompose phenotypic variance and covariance into additive genetic (A), shared environmental (C), and nonshared environmental (E) etiologies (11).

We began by comparing intraclass correlations for MZ and DZ twins. To the extent that MZ twins correlate more highly than DZ twins, genetic influences (A) are implied. Shared environmental effects (C) are inferred from the residual familial resemblance not explained by heritability and can be estimated by subtracting the estimate of heritability from the MZ correlation. The difference between the MZ twin correlation and unity represents an estimate of nonshared environmental effects and measurement error (E). The ACE model parameters, together with confidence intervals, can be calculated more accurately using structural equation modeling with maximum-likelihood estimation, which also provides formal model fit statistics (70). Models were fit using the structural equation modeling program OpenMx (71). All fit statistics are available from the corresponding author on request.

Bivariate genetic analysis of covariance between variables is an extension of the univariate genetic analysis of variance. MZ and DZ cross-trait cross-twin correlations are examined to decompose the covariance between traits into additive genetic (A), shared environmental (C), and nonshared environmental (E) components. The bivariate genetic model estimates genetic and environmental mediation of the phenotypic correlation between variables (Fig. S1). Central to bivariate genetic analysis is the genetic correlation, which is the extent to which genetic effects on one variable are correlated with genetic effects on another variable, which is an index of pleiotropy. Genetic mediation of the phenotypic correlation between two variables is the genetic correlation weighted by the heritabilities of the two variables (Fig. S1*A*). An alternative representation of bivariate model-fitting is Cholesky decomposition (Fig. S1*B*), which focuses on how much of the variance of one variable can be accounted for by another variable, which is well suited to addressing our central question of the extent to which the heritability of GCSE can be explained by each of the nine predictor domains.

A series of nine bivariate analyses addressed the question of how much of the phenotypic variance and how much of the heritability of GCSE scores can be explained by each of the domains. Additionally, the proportion of phenotypic correlation between the GCSE core measure and nine domains was decomposed into additive genetic (A), shared environmental (C), and nonshared environmental (E) factors. This series of bivariate analyses did not control for variance explained by the other domains. Therefore, the phenotypic and genetic variance in GCSE explained by these individual bivariate analyses was expected to exceed 100% across the nine domains. A multivariate genetic extension of Cholesky analysis was used to estimate the extent to which the nine domains jointly explain the heritability of GCSE, taking into account the covariance among the nine domains.

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1. OECD (2013) *Education at a Glance 2013* (Organisation for Economic Co-operation and Development, Paris).
2. Bronfenbrenner U (1996) *The State of Americans: This Generation and the Next* (Simon and Schuster, New York).
3. Cutler DM, Lleras-Muney A (2008) *Making Americans Healthier: Social and Economic Policy as Health Policy*, eds Schoeni RF, House JS, Kaplan GA, Pollack H (Russell Sage Foundation, New York).
4. Cutler DM, Lleras-Muney A (2012) *Education and Health: Insights from International Comparisons* (National Bureau of Economic Research, Cambridge, MA).
5. Caprara GV, Barbaranelli C, Pastorelli C, Bandura A, Zimbardo PG (2000) Prosocial foundations of children's academic achievement. *Psychol Sci* 11(4):302–306.
6. Buchmann C, Dalton B (2002) Interpersonal influences and educational aspirations in 12 countries: The importance of institutional context. *Sociol Educ* 75(2): 99–122.

7. Asbury K, Plomin R (2013) *G is for Genes: The Impact of Genetics on Education and Achievement* (Wiley-Blackwell, Chichester, UK).
8. Nye B, Konstantopoulos S, Hedges LV (2004) How large are teacher effects? *Educ Eval Policy Anal* 26(3):237–257.
9. Gill CE, Jardine R, Martin NG (1985) Further evidence for genetic influences on educational achievement. *Br J Educ Psychol* 55(Pt 3):240–250.
10. Martin NG, Martin PG (1975) The inheritance of scholastric abilities in a sample of twins. I. Ascertainments of the sample and diagnosis of zygosity. *Ann Hum Genet* 39(2):213–218.
11. Plomin R, DeFries JC, Knopik VS, Neiderhiser JM (2013) *Behavioral Genetics* (Worth Publishers, New York), 6th Ed.
12. Kovas Y, et al. (2013) Literacy and numeracy are more heritable than intelligence in primary school. *Psychol Sci* 24(10):2048–2056.
13. Shakeshaft NG, et al. (2013) Strong genetic influence on a UK nationwide test of educational achievement at the end of compulsory education at age 16. *PLoS ONE* 8(12):e80341.
14. Alloway TP, Alloway RG (2010) Investigating the predictive roles of working memory and IQ in academic attainment. *J Exp Child Psychol* 106(1):20–29.
15. Deary IJ, Strand S, Smith P, Fernandes C (2007) Intelligence and educational achievement. *Intelligence* 35(1):13–21.
16. Gathercole SE, Pickering SJ, Knight C, Stegmann Z (2004) Working memory skills and educational attainment: Evidence from national curriculum assessments at 7 and 14 years of age. *Appl Cogn Psychol* 18(1):1–16.
17. Mackintosh N (2011) *IQ and Human Intelligence* (Oxford Univ Press, Oxford, UK).
18. Diseth Å (2011) Self-efficacy, goal orientations and learning strategies as mediators between preceding and subsequent academic achievement. *Learn Individ Differ* 21(2):191–195.
19. Eccles JS, Roeser R, Wigfield A, Freedman-Doan C (1999) *Child Psychology: A Handbook of Contemporary Issues*, eds Balter L, Tamis-LeMonda CS (Psychology Press, Philadelphia), pp 287–317.
20. Spinath B, Spinath FM, Harlaar N, Plomin R (2006) Predicting school achievement from general cognitive ability, self-perceived ability, and intrinsic value. *Intelligence* 34(4): 363–374.
21. Zuffianò A, et al. (2013) Academic achievement: The unique contribution of self-efficacy beliefs in self-regulated learning beyond intelligence, personality traits, and self-esteem. *Learn Individ Differ* 23:158–162.
22. Downey LA, Mountstephen J, Lloyd J, Hansen K, Stough C (2008) Emotional intelligence and scholastic achievement in Australian adolescents. *Aust J Psychol* 60(1): 10–17.
23. Mavroveli S, Sánchez-Ruiz MJ (2011) Trait emotional intelligence influences on academic achievement and school behaviour. *Br J Educ Psychol* 81(Pt 1):112–134.
24. Parker JDA, et al. (2004) Academic achievement in high school: Does emotional intelligence matter? *Pers Individ Dif* 37(7):1321–1330.
25. Pope D, Roper C, Qualter P (2012) The influence of emotional intelligence on academic progress and achievement in UK university students. *Assess Eval High Educ* 37(8):907–918.
26. Briley DA, Domiteaux M, Tucker-Drob EM (2014) Achievement-relevant personality: Relations with the Big Five and validation of an efficient instrument. *Learn Individ Differ* 32:26–39.
27. Laidra K, Pullmann H, Allik J (2007) Personality and intelligence as predictors of academic achievement: A cross-sectional study from elementary to secondary school. *Pers Individ Dif* 42(3):441–451.
28. Stankov L (2013) Noncognitive predictors of intelligence and academic achievement: An important role of confidence. *Pers Individ Dif* 55(7):727–732.
29. Tough P (2013) *How Children Succeed* (Random House, London, UK).
30. Marques SC, Pais-Ribeiro JL, Lopez SJ (2011) The role of positive psychology constructs in predicting mental health and academic achievement in children and adolescents: A two-year longitudinal study. *J Happiness Stud* 12(6):1049–1062.
31. Senko C, Hulleman CS, Harackiewicz JM (2011) Achievement goal theory at the crossroads: Old controversies, current challenges, and new directions. *Educ Psychol* 46(1):26–47.
32. von Stumm S, Hell B, Chamorro-Premuzic T (2011) The hungry mind: Intellectual curiosity is the third pillar of academic performance. *Perspect Psychol Sci* 6(6):574–588.
33. Blackwell LS, Trzesniewski KH, Dweck CS (2007) Implicit theories of intelligence predict achievement across an adolescent transition: A longitudinal study and an intervention. *Child Dev* 78(1):246–263.
34. Zimmerman BJ, Bandura A, Martinez-Pons M (1992) Self-motivation for academic attainment: The role of self-efficacy beliefs and personal goal setting. *Am Educ Res J* 29(3):663–676.
35. Hinshaw SP (1992) Externalizing behavior problems and academic underachievement in childhood and adolescence: Causal relationships and underlying mechanisms. *Psychol Bull* 111(1):127–155.
36. Pingault J-B, et al. (2011) Childhood trajectories of inattention and hyperactivity and prediction of educational attainment in early adulthood: A 16-year longitudinal population-based study. *Am J Psychiatry* 168(11):1164–1170.
37. De Ridder KAA, et al. (2013) Adolescent health and high school dropout: A prospective cohort study of 9000 Norwegian adolescents (the Young-HUNT). *PLoS ONE* 8(9):e74954.
38. Hill NE, Tyson DF (2009) Parental involvement in middle school: A meta-analytic assessment of the strategies that promote achievement. *Dev Psychol* 45(3):740–763.
39. Marchant GJ, Paulson SE, Rothlisberg BA (2001) Relations of middle school students' perceptions of family and school contexts with academic achievement. *Psychol Sch* 38(6):505–519.
40. Leeson P, Ciarrochi J, Heaven PCL (2008) Cognitive ability, personality, and academic performance in adolescence. *Pers Individ Dif* 45(7):630–635.
41. Roskam I, Nils F (2007) Predicting intra-individual academic achievement trajectories of adolescents nested in class environment: Influence of motivation, implicit theory of intelligence, self-esteem and parenting. *Psychol Belg* 47(1):119–143.
42. Schmidt FL (2014) A general theoretical integrative model of individual differences in interests, abilities, personality traits, and academic and occupational achievement: A commentary on four recent articles. *Perspect Psychol Sci* 9(2):211–218.
43. Bartels M, Rietveld MJH, Van Baal GCM, Boomsma DI (2002) Heritability of educational achievement in 12-year-olds and the overlap with cognitive ability. *Twin Res* 5(6):544–553.
44. Calvin CM, et al. (2012) Multivariate genetic analyses of cognition and academic achievement from two population samples of 174,000 and 166,000 school children. *Behav Genet* 42(5):699–710.
45. Johnson W, Deary IJ, Iacono WG (2009) Genetic and environmental transactions underlying educational attainment. *Intelligence* 37(5):466–478.
46. Kovas Y, Haworth CMA, Dale PS, Plomin R (2007) The genetic and environmental origins of learning abilities and disabilities in the early school years. *Monogr Soc Res Child Dev* 72(3):vii, 1–144.
47. Petrill SA, Wilkerson B (2000) Intelligence and achievement: A behavioral genetic perspective. *Educ Psychol Rev* 12(2):185–199.
48. Thompson LA, Detterman DK, Plomin R (1991) Associations between cognitive abilities and scholastic achievement: Genetic overlap but environmental differences. *Psychol Sci* 2(3):158–165.
49. Wadsworth SJ, DeFries JC, Fulker DW, Plomin R (1995) Cognitive ability and academic achievement in the Colorado Adoption Project: A multivariate genetic analysis of parent-offspring and sibling data. *Behav Genet* 25(1):1–15.
50. Wainwright MA, Wright MJ, Geffen GM, Luciano M, Martin NG (2005) The genetic basis of academic achievement on the Queensland Core Skills Test and its shared genetic variance with IQ. *Behav Genet* 35(2):133–145.
51. Greven CU, Harlaar N, Kovas Y, Chamorro-Premuzic T, Plomin R (2009) More than just IQ: school achievement is predicted by self-perceived abilities—but for genetic rather than environmental reasons. *Psychol Sci* 20(6):753–762.
52. Gottschling J, Spengler M, Spinath B, Spinath FM (2012) The prediction of school achievement from a behavior genetic perspective: Results from the German twin study on Cognitive Ability, Self-Reported Motivation, and School Achievement (CoSMoS). *Pers Individ Dif* 53(4):381–386.
53. Spinath FM, Spinath B, Plomin R (2008) The nature and nurture of intelligence and motivation in the origins of sex differences in elementary school achievement. *Eur J Pers* 22(3):211–229.
54. Hicks BM, Johnson W, Iacono WG, McGue M (2008) Moderating effects of personality on the genetic and environmental influences of school grades helps to explain sex differences in scholastic achievement. *Eur J Pers* 22(3):247–268.
55. Johnson W, McGue M, Iacono WG (2005) Disruptive behavior and school grades: Genetic and environmental relations in 11-year-olds. *J Educ Psychol* 97(3):391–405.
56. Newsome J, Boisvert D, Wright JP (2014) Genetic and environmental influences on the co-occurrence of early academic achievement and externalizing behavior. *J Crim Justice* 42(1):45–53.
57. Polderman TJC, Boomsma DI, Bartels M, Verhulst FC, Huizink AC (2010) A systematic review of prospective studies on attention problems and academic achievement. *Acta Psychiatr Scand* 122(4):271–284.
58. Saudino KJ, Plomin R (2007) Why are hyperactivity and academic achievement related? *Child Dev* 78(3):972–986.
59. Hanscombe KB, Haworth CMA, Davis OSP, Jaffee SR, Plomin R (2011) Chaotic homes and school achievement: A twin study. *J Child Psychol Psychiatry* 52(11):1212–1220.
60. Haworth CMA, et al. (2013) Understanding the science-learning environment: A genetically sensitive approach. *Learn Individ Differ* 23:145–150.
61. Johnson W, McGue M, Iacono WG (2006) Genetic and environmental influences on academic achievement trajectories during adolescence. *Dev Psychol* 42(3):514–532.
62. Haworth CMA, Davis OSP, Plomin R (2013) Twins Early Development Study (TEDS): A genetically sensitive investigation of cognitive and behavioral development from childhood to young adulthood. *Twin Res Hum Genet* 16(1):117–125.
63. Vinkhuyzen AA, van der Sluis S, Maes HH, Posthuma D (2012) Reconsidering the heritability of intelligence in adulthood: Taking assortative mating and cultural transmission into account. *Behav Genet* 42(2):187–198.
64. Sahlberg P (2011) *Finnish Lessons: What Can the World Learn from Educational Change in Finland?* (Teachers College Press, New York).
65. Heath AC, et al. (1985) Education policy and the heritability of educational attainment. *Nature* 314(6013):734–736.
66. Price TS, et al. (2000) Infant zygosity can be assigned by parental report questionnaire data. *Twin Res* 3(3):129–133.
67. McGue M, Bouchard TJ, Jr (1984) Adjustment of twin data for the effects of age and sex. *Behav Genet* 14(4):325–343.
68. Lehmann E (1975) *Nonparametric Statistical Methods Based on Ranks* (Holden-Day, San Francisco).
69. Van Der Waerden BL (1975) On the sources of my book Moderne Algebra. *Hist Math* 2(1):31–40.
70. Rijsdijk FV, Sham PC (2002) Analytic approaches to twin data using structural equation models. *Brief Bioinform* 3(2):119–133.
71. Boker S, et al. (2011) OpenMx: An open source extended structural equation modeling framework. *Psychometrika* 76(2):306–317.

Chapter 5: True grit and genetics: Predicting academic achievement from personality

This chapter, using personality to predict educational achievement, is presented as a published paper. It is an exact copy of this publication.

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True Grit and Genetics: Predicting Academic Achievement From Personality

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Grit—perseverance and passion for long-term goals—has been shown to be a significant predictor of academic success, even after controlling for other personality factors. Here, for the first time, we use a U.K.-representative sample and a genetically sensitive design to unpack the etiology of Grit and its prediction of academic achievement in comparison to well-established personality traits. For 4,642 16-year-olds (2,321 twin pairs), we used the Grit-S scale (perseverance of effort and consistency of interest), along with the Big Five personality traits, to predict grades on the General Certificate of Secondary Education (GCSE) exams, which are administered U.K.-wide at the end of compulsory education. Twin analyses of Grit perseverance yielded a heritability estimate of 37% (20% for consistency of interest) and no evidence for shared environmental influence. Personality, primarily conscientiousness, predicts about 6% of the variance in GCSE grades, but Grit adds little to this prediction. Moreover, multivariate twin analyses showed that roughly two-thirds of the GCSE prediction is mediated genetically. Grit perseverance of effort and Big Five conscientiousness are to a large extent the same trait both phenotypically ($r = 0.53$) and genetically (genetic correlation = 0.86). We conclude that the etiology of Grit is highly similar to other personality traits, not only in showing substantial genetic influence but also in showing no influence of shared environmental factors. Personality significantly predicts academic achievement, but Grit adds little phenotypically or genetically to the prediction of academic achievement beyond traditional personality factors, especially conscientiousness.

Keywords: Grit, perseverance, personality, academic achievement, twin study

Academic achievement at the end of compulsory schooling is of major importance to individuals, their families, and society. For example, in the United Kingdom, the results of national standardized examinations (General Certificate of Secondary Education [GCSE]) taken at age 16 are used to make decisions regarding further education and future employment. Understanding the correlates and predictors of differences among children in their academic achievement at the end of compulsory education could have important implications for educational curricula decisions and possible educational interventions.

Extraversion, Agreeableness, Conscientiousness, Openness, and Neuroticism form the broad five dimensions of personality. The Big Five personality factors represent a central approach to the trait theory of personality. They constitute an empirically verified taxonomy of traits, which has been derived empirically as a reasonably comprehensive broad-stroke overview of human personality, with most other finer grained personality measures like effort, willpower, and persistence, encompassed by these five personality facets (Briley, Domiteaux, & Tucker-Drob, 2014; McCabe, Van Yperen, Elliot, & Verbraak, 2013). The Big Five personality factors—especially Conscientiousness, Agreeableness, and Neuroticism (negatively)—predict academic achievement, explaining a significant but modest proportion of variance in achievement (Chamorro-Premuzic & Furnham, 2003; Conard,

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2006; Laidra, Pullmann, & Allik, 2007; Noftle & Robins, 2007; Poropat, 2009). Of all personality factors, Conscientiousness is the most robust predictor of academic achievement across education, with an average correlation of 0.20 (Noftle & Robins, 2007; Poropat, 2009; Richardson, Abraham, & Bond, 2012; Trapmann, Hell, Hirn, & Schuler, 2007; Vedel, 2014; Wagerman & Funder, 2007). In one meta-analysis, Openness also significantly predicted university grades ($r = 0.12$; Poropat, 2009), but another meta-analysis found that only Conscientiousness significantly predicted university grades (Trapmann et al., 2007). There is some evidence that Openness predicts secondary school achievements, such as university entrance exams, but that it is a weaker predictor of success at university (Noftle & Robins, 2007).

Although there is strong evidence for the association between personality factors and achievement, some research suggests that narrower facets of personality, more specific than the Big Five, such as effort and intellectual investment, predict more variance in achievement than the major Big Five personality factors (Briley, Domiteaux, & Tucker-Drob, 2014; Paunonen, Haddock, Forsterling, & Keinonen, 2003; Paunonen & Jackson, 2000). However, such specific traits are usually subsumed within the Big Five factors as lower level traits (Paunonen, Haddock, Forsterling, & Keinonen, 2003). Focusing on these narrower, more specific facets may increase the predictive power as they may explain more variance in the outcomes than the broad Big Five (Briley, Domiteaux, & Tucker-Drob, 2014; Paunonen, Haddock, Forsterling, & Keinonen, 2003; Paunonen & Jackson, 2000).

Grit might be one of these narrower facets of personality that predict school achievement. *Grit*—perseverance and passion for long-term goals, as defined by Duckworth, Peterson, Matthews, & Kelly (2007)—has emerged in recent years as a significant predictor of life success and school achievement (Duckworth et al., 2007). Although Grit is closely related to Conscientiousness (phenotypic correlations around .70), some evidence suggests that Conscientiousness is multifaceted (Eskreis-Winkler, Shulman, Beal, & Duckworth, 2014), so whereas Grit is not identical to Conscientiousness it might be very similar to facets of Conscientiousness, such as industriousness and perseverance. Studies suggest that a more fine-grained measure of Conscientiousness like Grit might increase the predictive usefulness of this personality facet (Duckworth et al., 2007; Eisenberg, Duckworth, Spinrad, & Valiente, 2014; MacCann, Duckworth, & Roberts, 2009). Indeed, Grit (comprising perseverance of effort and consistency of interests) has been found to predict life success such as job retention, graduation from high school and scholastic achievement across the life span because it refers to extreme stamina and effort (Eskreis-Winkler, Shulman, Beal, & Duckworth, 2014). Grit remains a significant predictor of life outcomes when controlling for Big Five personality factors, although it explains only minor incremental variance (Duckworth, 2013; Duckworth & Eskreis-Winkler, 2013; Duckworth et al., 2007; Eskreis-Winkler et al., 2014; Von Culin, Tsukayama, & Duckworth, 2014).

A critical limitation of most research studying Grit has been the use of highly selected populations such as undergraduate students, spelling competition finalists, cadets, and teachers; research on less restricted samples might yield higher correlations. Moreover, despite the evidence for Grit's significant prediction of educational achievement, more attention to the effect size and distinctiveness of this prediction is warranted prior to considering intervention. Some researchers have suggested that Grit might be more malleable than socioeconomic status, intelligence, and other predictors of academic achievement (Duckworth & Gross, 2014). It is often assumed that its origins lie with family values and thus would be more amenable to training (Duckworth & Gross, 2014) as compared with cognitive factors or socioeconomic status, which are considered to be very difficult to amend (Moffitt et al., 2011). However, these assumptions may be premature for three reasons. First, all personality traits show similar heritability. Second, previous research suggests that it is nonshared environment (environmental influences that do not contribute to similarities between siblings growing up in the same family and attending the same school) and not shared environment that is important for personality traits (Turkheimer, Pettersson, & Horn, 2013). Third, we are not aware of studies that have shown the effects of training Grit. Despite the lack of empirical evidence training Grit has been set as a priority by the U.S. Department of Education (see http://edf.stanford.edu/readings/download-promotings-grit-tenacity-and-perseverance-report) and the U.K. Department for Education (see https://www.gov.uk/government/news/england-to-become-a-global-leader-of-teaching-character). The effectiveness of training programs should be rigorously researched before they are rolled out widely.

Little is known about why children differ in Grit or about the etiology of its correlates with educational achievement. Although there has as yet been no genetically sensitive study investigating the etiology of Grit or its links with school achievement, twin studies investigating the associations between Big Five traits and educational achievement have found that these associations are largely explained by genetic factors rather than environmental factors (Krapohl et al., 2014; Luciano, Wainwright, Wright, & Martin, 2006).

Given the potential impact of Grit on educational policy in the United Kingdom and the United States, it is vital to understand this trait more fully. Here, for the first time, we investigate the genetic and environmental origins of individual differences in Grit within a large representative U.K. sample of 16-year-olds. We also consider the power of Grit to predict academic achievement beyond the Big Five personality traits and the extent to which this prediction is mediated by genetic and environmental factors.

Method

Participants

The present study used the Twins Early Development Study (TEDS) sample, which is a large longitudinal study that recruited over 16,000 twin pairs born in England and Wales between 1994 and 1996 (Haworth, Davis, & Plomin, 2013). Although there has been some attrition, more than 10,000 twin pairs remain actively involved in the study. Rich data have been collected over many years on cognitive and learning abilities, personality, and behavior. It is important to note that in relation to the highly selected nature of samples used in previous research, the present sample is representative of the U.K. population (Haworth, Davis, & Plomin, 2013; Kovas, Haworth, Dale, & Plomin, 2007).

The present study included 4,642 TEDS participants (2,321 twin pairs) from whom Grit, Big Five personality factors and GCSE scores were available. The sample size for each measure is shown in the results. Children who had major medical or psychiatric problems were excluded from the analyses. Zygosity was assessed using a parent questionnaire of physical similarity, which is 95% accurate when compared with DNA testing (Price et al., 2000). DNA testing was conducted when zygosity was not clear from the physical similarity criteria. Both same-sex twin pairs and opposite-sex twin pairs were included in the study, with the overall sample including 883 monozygotic (MZ) pairs, 761 same-sex dizygotic (DZ) twin pairs and 677 opposite-sex DZ twin pairs.

Measures

Grit was assessed at age 16 using the Grit-S questionnaire with online administration (Duckworth & Quinn, 2009). The Grit-S includes eight items and is scored on two scales, perseverance of effort (four items) and consistency of interest (four items). Twins were asked, "To what extent do the following statements describe you?" Participants were asked to rate the statements on a 5-point scale ranging from from 1 (*very much like me*) to 5 (*not like me at all*). For example, a perseverance item was "Setbacks don't discourage me" and a consistency of interest item was "I have difficulty maintaining my focus on projects that take more than a few months to complete (reversed)." Both subscales have been shown to have reasonable reliability; in the present study, Cronbach alphas for consistency of interest and perseverance of effort were .73 and .63.

Personality was measured using the abbreviated questionnaire of the five-factor model—Five-Factor Model Rating Form (FFMRF), which was administered online (Mullins-Sweatt, Jamerson, Samuel, Olson, & Widiger, 2006). The FFMRF consists of 30 items, with six items for each of the five personality traits. Twins were asked to rate themselves on a 5-point scale on which 1 = *extremely low*, 2 = *low*, 3 = *nether high nor low*, 4 = *high*, and 5 = *extremely high*. For example, the Conscientiousness item of self-discipline was rated from dogged/devoted to hedonistic/negligent; the Neuroticism item of depressiveness was rated from pessimistic/glum to optimistic. The FFMRF has been reported to be reliable (Samuel, Mullins-Sweatt, & Widiger, 2013); in our sample, Cronbach alphas were .78 for Conscientiousness, .68 for Neuroticism, .70 for Extraversion, .63 for Openness, and .68 for Agreeableness.

Educational achievement was assessed by the GCSE, a U.K.-wide national exam administered at the end of compulsory schooling, usually at age 16. Students typically start GCSE courses at the age of 14 and can choose from a variety of courses such as history, music, physical education, and modern foreign languages, although English, mathematics, and science are compulsory. The exams are graded from A* to G, with a U grade given for failed exams. Grades were coded from 11 (A*) to 4 (G) to create equivalent numerical comparisons. No information about failed courses was available. Most pupils receive five or more grades between A* and C, which is the requirement for further education in the United Kingdom. GCSE grades were obtained from parents or the twins themselves via questionnaires sent in by mail or conducted over the telephone. For 7,367 twins, the grades were verified using the National Pupil Database (NPD; https://www.gov.uk/government/uploads/system/uploads/attachment_data/file/251184/SFR40_2013_FINALv2.pdf), and yielded a correlation with parent- and twin-reported grades of 0.99 for mathematics, 0.98 for English and >0.95 for all the sciences.

We created a mean composite measure of core academic subjects: English (English language or English literature grade), mathematics and sciences (single- or double weighted science; or when taken separately, physics, chemistry, and biology grade). The mean of these core GCSE exam grades was used as a general index of academic achievement at the end of compulsory education.

Analyses

Phenotypic analyses. We compared means and variance for boys and girls and for MZ and DZ twins. Mean differences for age and sex and their interaction were tested using univariate analysis of variance (ANOVA).

Correlation was used to estimate associations between the two Grit-S subscales (perseverance of effort and consistency of interest), the Big Five personality scales, and GCSE grades. Principal component analyses were used to assess the factor structure of Grit-S scale.

Multiple regression assessed the extent to which Grit-S perseverance of effort and consistency of interest predict GCSE grades. Hierarchical multiple regression tested the incremental prediction of GCSE grades from the two Grit subscales when Big Five personality factors were entered as the first step in the regression model. Because the present sample was a twin sample, we maintained independence of data by randomly selecting one twin per pair for all phenotypic analyses.

Twin analyses. The twin method was used to estimate the relative contribution of additive genetic (A), shared environmental (C) and nonshared environmental (E) components of variance. The twin method compares the resemblance for MZ twins, who share 100% of their genes, to DZ twins who share on average 50% of their segregating genes (Plomin, DeFries, Knopik, & Neiderhiser, 2013). If MZ correlations are larger than DZ correlations, genetic influence can be inferred. Shared environmental influences are assumed to be the same for both MZ and DZ twins growing up in the same household. Nonshared environmental influences are unique to individuals, and do not contribute to similarities between twins; importantly this component of variance also includes the measurement of error. A can be calculated approximately by doubling the difference between MZ and DZ correlations, C can be calculated by deducting the heritability estimate from the MZ correlations, and E can be calculated by deducting the MZ correlation from unity (Rijsdijk & Sham, 2002). These ACE parameters can be calculated more accurately and with confidence intervals using structural equation models with maximum likelihood estimation. The data were analyzed using the structural equation modeling program OpenMx (Boker et al., 2011).

Bivariate genetic analysis extends univariate ACE analysis to the covariance between two traits. The ACE parameters can be estimated for the covariance between traits by comparing the cross-twin cross-trait correlations (Twin 1 score on Trait A with Twin 2 score on Trait B) for MZ and DZ twin pairs. The extent to which these MZ correlations exceed DZ correlations indexes genetic mediation of the phenotypic correlation between the two traits. The contributions of C and E to the phenotypic correlation can also be estimated.

Table 1
Descriptive Statistics: Means (Standard Deviations in Parentheses) for Grit Consistency of Interest, Grit Perseverance of Effort, and Big Five Personality Factors

Personality trait	n	Whole sample	Male	Female	MZm	DZm	MZf	DZf	DZos	Sex	Zygosity	Sex × Zygosity	R^2
Grit Consistency of Interest	4,849	2.85 (.80)	2.75 (.81)	2.95 (.81)	2.75 (.81)	2.70 (.81)	3.01 (.82)	2.93 (.82)	2.84 (.79)	31.08**	2.19	1.48	.02
Grit Perseverance	4,850	3.73 (.62)	3.71 (.62)	3.73 (.62)	3.78 (.59)	3.71 (.61)	3.76 (.63)	3.70 (.61)	3.68 (.63)	.23	7.64*	.72	<.01
Extraversion	4,782	3.65 (.63)	3.62 (.63)	3.68 (.62)	3.67 (.62)	3.62 (.62)	3.66 (.63)	3.68 (.60)	3.65 (.64)	3.12	.33	1.32	<.01
Openness	4,779	3.65 (.63)	3.56 (.61)	3.59 (.58)	3.58 (.63)	3.54 (.61)	3.57 (.58)	3.59 (.59)	3.58 (.58)	.70	.10	1.20	<.01
Agreeableness	4,771	3.67 (.58)	3.54 (.57)	3.75 (.59)	3.56 (.58)	3.50 (.58)	3.76 (.58)	3.73 (.60)	3.66 (.59)	59.48**	1.15	.02	.03
Conscientiousness	4,768	3.72 (.62)	3.64 (.62)	3.78 (.62)	3.76 (.63)	3.67 (.61)	3.82 (.60)	3.74 (.65)	3.67 (.62)	22.63**	5.14*	.68	.01
Neuroticism	4,786	2.58 (.68)	2.47 (.64)	2.65 (.67)	2.41 (.58)	2.49 (.67)	2.64 (.72)	2.70 (.63)	2.56 (.66)	44.14**	2.95	5.96*	.02

Note. For the results in the last four columns: F statistics; R^2 = proportion of the variance explained by the combined effects of sex, zygosity, and their interaction. n = sample size after exclusions (individuals); MZm = monozygotic male; DZm = dizygotic male; MZf = monozygotic female; DZf = dizygotic female; DZos = dizygotic opposite sex.
* $p < .05$. ** $p < .01$.

Bivariate genetic analysis yields an additional set of statistics, including the genetic correlation (r_G), which indicates the extent to which the same genes influence two traits regardless of their heritabilities. In other words, the heritability of two traits could be low, but the genetic correlation between the traits could be high. The genetic correlation indexes the extent to which genetic influences on one trait also impact the other trait (Plomin, DeFries, Knopik, & Neiderhiser, 2013). Roughly speaking, the genetic correlation indicates the chance that a genetic variant associated with one trait is also associated with the other trait. The genetic correlation implies causality in the sense that it indexes the extent to which the same genes affect both traits; although the current method does not provide information on the possible underlying mechanisms (Ligthart & Boomsma, 2012). Similarly, bivariate analysis estimates the shared environmental correlation (r_C) and the nonshared environmental correlation (r_E). A shared environmental correlation of 1.0 indicates that the shared environmental influences that make twins similar for one trait also make twins similar on the other trait. Similarly, for nonshared environment, a correlation of zero indicates that completely different nonshared environmental influences affect two traits (Plomin, DeFries, Knopik, & Neiderhiser, 2013).

Results

Phenotypic Analyses

Table 1 presents mean scores and standard deviations for five groups: MZ males, MZ females, DZ males, DZ females, and DZ opposite-sex twin pairs. ANOVA results conducted after randomly selecting one twin per pair, show that sex, zygosity and their interaction explain only around 1% of the variance on average.

Factor analysis was used to assess the factors structure of the Grit-S scale. Table 2 illustrates the factor loadings using oblique factor rotations, which suggests that the two-factor model fits the Grit data best. The factor structure was virtually identical when we tested this in the other half of the data (we randomly assigned members of each twin pair to two subsamples). The two Grit subscales, consistency of interest and perseverance of effort, in the present representative sample of 16-year-olds in the United Kingdom correlate less than previously reported ($r = 0.29$, $p < .001$). For these reasons, subsequent analyses were conducted for the two subscales separately rather than combining them as is often done.

Table 3 presents correlations among all measures. Conscientiousness and Grit perseverance correlated most highly with GCSE scores ($r = 0.24$ and 0.17, respectively). Grit perseverance was

Table 2
Factor Loadings for Grit-S Scale Using Direct Oblim Rotation

Grit scale item	Direct Oblim rotation with Kaiser normalization pattern matrix: Consistency of Interest	Perseverance of Effort
New ideas and projects sometimes distract me from previous ones (reversed)	.73	−.09
Setbacks don't discourage me	−.04	.63
I have been obsessed with a certain idea or project for a short time but later lost interest (reversed)	.78	−.06
I am a hard worker	.06	.74
I often set a goal but later choose to pursue a different one (reversed)	.75	.01
I have difficulty maintaining my focus on projects that take more than a few months to complete	.68	.25
I finish whatever I begin	.28	.64
I am diligent	−.15	.71

Table 3
Phenotypic Correlations Between Two Grit Subscales, Big Five Personality Factors, and GCSE Scores (95% Confidence Intervals in Parentheses)

Factor or subscale	C	N	E	O	A	CoI	P	GCSE
Conscientiousness (C)	—							
Neuroticism (N)	−.18 (−.20, −.15)	—						
Extraversion (E)	.20 (.17, .23)	−.38 (−.41, −.35)	—					
Openness (O)	.06 (.03, .09)	−.06 (−.09, −.03)	.22 (.19, .25)	—				
Agreeableness (A)	.29 (.26, .29)	−.19 (−.21, −.16)	.15 (.12, .18)	.20 (.17, .23)	—			
Consistency of Interest (CoI)	.28 (.25, .30)	−.19 (−.21, −.16)	.07 (.04, .10)	−.10 (−.13, −.07)	.10 (.09, .13)	—		
Perseverance (P)	.53 (.50, .55)	−.31 (−.36, −.28)	.27 (.24, .30)	.08 (.05, .08)	.18 (.15, .20)	.29 (.26, .31)	—	
GCSE score	.24 (.21, .27)	.02 (−.01, .05)	.04 (.01, .07)	.09 (.05, .12)	.03 (.01, .07)	.06 (.03, .09)	.17 (.13, .20)	1.00

Note. GCSE = General Certificate of Secondary Education exams.

substantially correlated with Big Five Conscientiousness (r = 0.53). Grit consistency of interest correlated only 0.06 with GCSE scores.

Table 4 summarizes results for multiple regression analyses that take into account the intercorrelations among the personality measures in their prediction of GCSE scores. Together, the two Grit-S subscales explained 2% of the variance in GCSE grades. Grit perseverance of effort significantly predicted GCSE independent of Grit consistency of interest but not vice versa.

Table 4 also includes results for the hierarchical multiple regression used to estimate the prediction of GCSE scores from Grit-S perseverance of effort and consistency of interest when Big Five personality factors (Extraversion, Openness, Agreeableness, Conscientiousness, Neuroticism) were entered into the regression model in the first step. Big Five personality factors explained 5.5% of the variance in GCSE grades. Adding the Grit-S subscales to the regression model increased the variance explained by only 0.5%.

Twin Analyses

Univariate genetic analyses. Table 5 shows the twin correlations for the Big Five and Grit personality factors and their cross-trait cross-twin correlations with GCSE grades.

Table 6 shows the ACE estimates for the two Grit subscales and the Big Five traits, which follow from the MZ and DZ twin correlations presented in Table 5. The Grit subscales yielded results similar to the Big Five traits: moderate heritability, negligible shared environmental influence, and substantial nonshared environmental influences. All personality measures at age 16 were significantly heritable, with heritability estimates explaining approximately one third of the variance (20% to 38%), whereas shared environmental influences were negligible and not significant and two thirds of the variance was explained by nonshared environmental influences (62% to 76%).

Bivariate genetic analyses. Figure 1 illustrates the results of bivariate analyses between the personality measures and GCSE grades, which follow from the MZ and DZ cross-trait cross-twin correlations shown in Table 4. Bivariate heritability can be calculated by the product of the square root of the heritability of variable 1, the square root of the heritability of variable 2 and the genetic correlation between the two variables. The proportion of variance explained by C and E is calculated the same way, using C and E (and rC and rE, respectively). In Figure 1, for example, the top bar shows that the phenotypic correlation between Grit perseverance and GCSE scores was 0.17; the bivariate heritability is 0.15. Thus, 88% of the phenotypic correlation (0.15/0.17) was mediated by genetic factors. The highest phenotypic correlation was between Big Five conscientiousness and GCSE grades (0.24); 67% of this correlation was mediated genetically (bivariate heritability of 0.16). The phenotypic correlations between other Big Five personality factors and exam performance were very small, but are presented in Figure 1 for completeness.

Table 7 presents the genetic correlations and shared and nonshared environmental correlations between the personality measures and GCSE grades. The highest genetic correlations between personality and GCSE grades emerged for Big Five Conscientiousness (0.36) and Grit perseverance (0.33). The genetic correlation of 0.86 between Big Five Conscientiousness and Grit perseverance indicates that to a large extent the same genes influence these two

Table 4
Regression Analyses Investigating the Predictors of GCSE Achievement From Personality Measures

Personality trait	F	R^2	β
Multiple regression	$F(2, 1975) = 23.28^{**}$	.02	
Consistency of Interest			−.01
Perseverance of Effort			.15**
Hierarchical regression			
Step 1	$F(5, 1912) = 22.15^{**}$	.055	
Neuroticism			.08*
Extraversion			.01
Openness			.07*
Agreeableness			−.05*
Conscientiousness			.23**
Step 2	$F(7, 1912) = 17.34^{**}$	.06	
	F change $(2,1905) = 5.09^{**}$	R^2 change = .005	
Neuroticism			.09**
Extraversion			.01
Openness			.07*
Agreeableness			−.05*
Conscientiousness			.19**
Consistency of Interest			−.02
Perseverance of Effort			.09**

Note. For the hierarchical multiple regression, variables were entered in the regression model in the following order: (Step 1) Big Five personality scales; (Step 2) Big Five personality scales and Grit. β = standardized beta value; R^2 = variance explained. GCSE = General Certificate of Secondary Education exams.
* $p < .05$. ** $p < .01$.

personality factors. Although some of the shared environmental correlations are very high, little weight can be placed on these estimates, because there is so little shared environmental variance (see Table 5).

Discussion

Using a large representative sample of the U.K. population, we found that personality factors explain around 6% of the variance in academic achievement at the end of compulsory education at age 16. However, at this stage of education Grit adds only 0.5% to the prediction of GCSE variance after accounting for the association between achievement and Big Five personality factors. We believe that these results should warrant concern with the educational policy directives in the United States and the United Kingdom (Shechtman, DeBarger, Dornsife, Rosier, & Yarnall, 2013).

Twin analyses, conducted for the first time in the present study, showed that Grit (perseverance of effort and consistency of interest), just as other personality factors (Turkheimer, Pettersson, & Horn, 2013), is moderately heritable, with genetic factors explain-

Table 5
Twin Correlations for Personality Factors and Cross Trait Cross-Twin Correlations With GCSE Results and Personality Factors (95% Confidence Intervals in Parentheses)

Personality trait	MZ correlation	DZ correlation	MZ cross-trait cross-twin correlation	DZ cross-trait cross-twin correlation
Perseverance of Effort	.35 (n = 776)	.17 (n = 1,211)	.18 (n = 757)	−.01 (n = 1,210)
	(.30, .42)	(.12, .23)	(.11, .24)	(−.06, .05)
Consistency of Interests	.24 (n = 781)	.15 (n = 1,219)	.04 (n = 760)	−.01 (n = 1,216)
	(.18, .31)	(.09, .20)	(-.03, .11)	(−.06, .05)
Conscientiousness	.34 (n = 755)	.07 (n = 1,167)	.19 (n = 747)	.03 (n = 1,194)
	(.28, .40)	(.008, .12)	(.12, .25)	(−.03, .08)
Neuroticism	.29 (n = 759)	.15 (n = 1,183)	.003 (n = 751)	.03 (n = 1,200)
	(.23, .36)	(.10, .22)	(-.08, .06)	(−.02, .09)
Extraversion	.39 (n = 751)	.14 (n = 1,173)	.11 (n = 743)	.03 (n = 1,198)
	(.32, .44)	(.08, .19)	(.03, .18)	(−.02, .09)
Openness	.35 (n = 757)	.08 (n = 1,176)	.08 (n = 748)	.02 (n = 1,199)
	(.29, .41)	(.03, .14)	(.01, .15)	(−.03, .08)
Agreeableness	.24 (n = 750)	.11 (n = 1,167)	.03 (n = 744)	−.02 (n = 1,190)
	(.18, .31)	(.05, .16)	(-.04, .10)	(−.07, .04)

Note. To increase power in the present analyses, the full sample was used, combining males and females and including opposite-sex pairs. GCSE = General Certificate of Secondary Education exams; MZ = monozygotic; DZ = dizygotic.

Table 6
Model Fitting Results for Univariate Analyses for Additive Genetic (A), Shared Environmental (C), and Nonshared Environmental (E) Components of Variance for Personality Factors (95% Confidence Intervals in Parentheses)

Personality factor	Variance components (95% CI)		
	A	C	E
Perseverance of Effort	.37 (.24, .42)	.00 (0, .10)	.63 (.58, .69)
Consistency of Interests	.20 (.03, .31)	.05 (0, .17)	.75 (.69, .82)
Conscientiousness	.30 (.24, .36)	0 (0, .04)	.70 (.64, .76)
Neuroticism	.27 (.10, .35)	.02 (0, .15)	.71 (.65, .77)
Extraversion	.38 (.30, .43)	.00 (0, .05)	.62 (.57, .68)
Openness	.31 (.24, .37)	0 (0, .04)	.69 (.63, .75)
Agreeableness	.24 (.11, .30)	.00 (0, .10)	.76 (.70, .82)

ing about a third of the variance. Shared environmental factors, which are factors that contribute to similarities between members of a twin pair growing up in the same family and attending the same schools, explained no significant variance in these scales. The majority of the variance in all personality factors was explained by nonshared environmental factors, which are the factors that do not contribute to similarities between twin pairs growing up in the same family and attending the same schools. It should be emphasized, however, that behavioral genetic results such as these describe components of variance in a particular population at a particular time. Specifically, heritability does not imply immutability. The most limiting finding, for any possible intervention, is that shared environmental influence is negligible. This means that current differences between families and schools explain little variance in the development of Grit. However, even this finding does not limit the possible effect of a novel intervention that is not currently part of the environmental variation.

The focus of this study was the relationship between personality and academic achievement. Big Five personality traits have been well studied and research has consistently shown that these traits explain a small but significant proportion of the variance in educational achievement (Chamorro-Premuzic & Furnham, 2003; Krapohl et al., 2014; Laidra et al., 2007; Luciano et al., 2006; Noftle & Robins, 2007; Poropat, 2009). It has been argued that narrower aspects of personality could explain a larger proportion of the variance in academic achievement than the well-studied Big Five factors, such as curiosity, self-control, or motivation (Briley et al., 2014). Grit could be one of these narrower facets, but the effect size of Grit as measured by the Grit-S in the present study was very small, especially when the association among the Big Five was accounted for. Thus, the association between achievement and personality is largely explained by the Big Five and Grit adds little to this relationship. We also found that Grit consistency of interest does not significantly predict school achievement. One possibility is that consistency of interest has both positive and negative effects on scholastic achievement. Although it is good to keep focused and interested in the task at hand, it is also sometimes more adaptive to focus on new ideas and projects without distraction from previous interest. The core finding is that Grit, especially the perseverance of effort subscale, is substantially correlated with Conscientiousness, both phenotypically (0.53) and genetically (0.86). The extent to which an individual can have different scores on these two traits stems largely from nonshared environment; this may result from some measure-specific measurement error or aspects of the environment that affect only one trait.

The present findings show that Grit adds little to the prediction of academic achievement when other personality factors are controlled. This does not exclude the possibility that other cognitive or noncognitive predictors are important correlates of academic success. For example, self-efficacy has consistently been shown to be associated with school achievement (Chamorro-Premuzic, Harlaar, Greven, & Plomin, 2010; Greven, Harlaar, Kovas, Chamorro-Premuzic, & Plomin, 2009; Luciano et al., 2006; Richardson et al., 2012; Zimmerman, Bandura, & Martinez-Pons, 1992). Specifically, we have recently shown that at the end of compulsory education self-efficacy correlates substantially (0.49) with GCSE grades, although this correlation is largely mediated by genetic factors (Krapohl et al., 2014). Curiosity, specifically intellectual engagement, has also been shown to be a significant predictor of school achievement—a hungry mind could be the driving force for effort and perseverance (von Stumm, Hell, & Chamorro-Premuzic, 2011). Another noncognitive factor that has consistently been

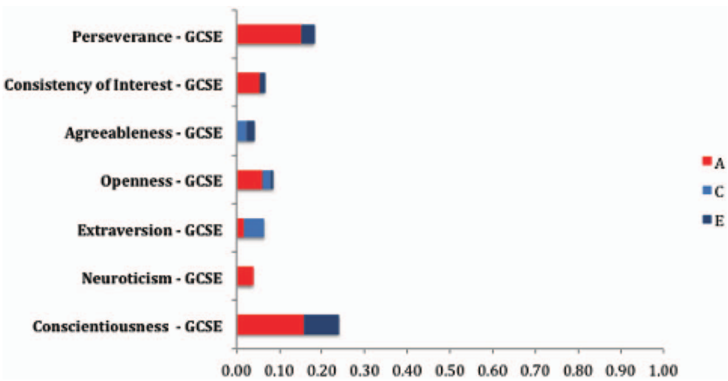

Figure 1. Bivariate estimates for additive genetic (A), shared environmental (C), and nonshared environmental (E) contributions to the correlations between personality measures and General Certificate of Secondary Education (GCSE) exam grades. The total length of the bar indicates the phenotypic correlations.

Table 7

Genetic (rG), Shared Environmental (rC) and Nonshared Environmental (rE) Correlations Between Grit, Big Five, and GCSE Exam Grades (95% Confidence Intervals in Parentheses)

	C	N	E	O	A	CoI	P	GCSE
				rG				
Conscientiousness (C)	—							
Neuroticism (N)	−.38 (−.69, −.36)	—						
Extraversion (E)	.44 (.28, .58)	−.61 (−.90, −.41)	—					
Openness (O)	.13 (−.04, .30)	−.07 (−.42, .17)	.09 (.03, .24)	—				
Agreeableness (A)	.47 (.23, .68)	−.27 (−.71, .13)	.16 (−.17, .39)	.21 (−.07, .48)	—			
Consistency of Interest (CoI)	.63 (.40, .87)	−.46 (−.76, −.46)	.41 (.16, .0.68)	−.19 (−.48, −.10)	.75 (.65, .96)	—		
Perserevance (P)	.86 (.76, 1.00)	−.37 (−.63, −.31)	.47 (.30, .68)	.06 (−.16, .17)	.46 (.19, .46)	.80 (.58, .96)	—	
GCSE core	.36 (.22, .52)	.10 (−.10, .32)	.04 (−.11, .18)	.14 (−.01, .29)	−.02 (−.25, .20)	.15 (.11–.37)	.33 (.17, .50)	—
				rC				
Conscientiousness (C)	—							
Neuroticism (N)	−.48 (−1.00, 1.00)	—						
Extraversion (E)	.68 (−.11, 1.00)	−.51 (−1.00, 1.00)	1.00					
Openness (O)	−.48 (−1.00, 1.00)	.59 (−1.00, 1.00)	.14 (−1.00, 1.00)	1.00				
Agreeableness (A)	.99 (−.05, 1.00)	−.49 (−1.00, 1.00)	.75 (−.74, 1.00)	−.40 (−1.00–1.00)	1.00			
Consistency of Interest (CoI)	−.97 (−1.00, 1.00)	.26 (−1.00, 1.00)	−.56 (−1.00, .88)	.42 (−1.00, 1.00)	−.95 (−.96, .16)	1.00		
Perserevance (P)	.48 (.31, .48)	−.81 (−1.00, 1.00)	.05 (−1.00, 1.00)	−.95 (−1.00, 1.00)	.42 (−1.00, 1.00)	−.34 (−1.00, 1.00)	1.00	
GCSE core	.15 (−.98, 1.00)	−.14 (−.14, 1.00)	.81 (−1.00, 1.00)	.66 (−1.00, 1.00)	.25 (−.47, .25)	−.06 (−.54, .62)	−.45 (−1.00, 1.00)	1.00
				rE				
Conscientiousness (C)	—							
Neuroticism (N)	−.10 (−.15, −.04)	—						
Extraversion (E)	.08 (.02, .14)	−.27 (−.33, −.21)	—					
Openness (O)	.03 (−.03, .09)	−.06 (−.12, −.06)	.30 (.24, .35)	—				
Agreeableness (A)	.23 (.17, .28)	−.15 (−.20, −.08)	.13 (.07, .19)	.21 (.15, .27)	—			
Consistency of Interest (CoI)	.18 (.12, .18)	−.12 (−.18, −.06)	−.04 (−.09, .02)	−.09 (−.15, −.03)	−.01 (−.05, .05)	—		
Perserevance (P)	.37 (.32, .42)	−.27 (−.26, −.21)	.17 (.11, .23)	.10 (.04, .16)	.07 (.06, .12)	.12 (.06, .18)	—	
GCSE score	.25 (.18, .32)	−.02 (−.09, .05)	−.08 (−.15, −.01)	.02 (−.05, .02)	.05 (−.02, .12)	.04 (−.04, .10)	.15 (.08, .23)	—

Note. GCSE = General Certificate of Secondary Education exams.

associated with academic achievement and life success is self-control—the capacity to regulate behavior and focus in the presence of temptation (Duckworth & Gross, 2014; Duckworth, Quinn, & Tsukayama, 2012; Duckworth, Tsukayama, & Kirby, 2013; Moffitt et al., 2011; Tangney, Baumeister, & Boone, 2004). Self-control has been shown to correlate highly with life success, even after controlling for other factors, such as intelligence and socioeconomic status, which might make it a good target for intervention (Moffitt et al., 2011). However, to our knowledge, no studies have specifically focused on the efficacy of training self-control. More research is needed to find how intervention programs could enhance self-control, or indeed any other noncognitive factors, during childhood, and whether this intervention could have a lasting effect.

Limitations of our study begin with the usual limitations of a twin study, such as the equal environment assumption or the assumption of random mating, as described in detail elsewhere (Plomin et al., 2013; Rijsdijk & Sham, 2002). It should also be noted that our results may be limited to age 16 and that Grit could play a larger role in academic success in university or postgraduate studies (Briley et al., 2014; Duckworth & Quinn, 2009). Indeed, research has shown that Grit increases with age and becomes increasingly important when individuals understand what their lifelong goals as well as their interests are (Duckworth & Eskreis-Winkler, 2013).

The results of the present study could also be affected by gene–environment interplay. As children grow older, they increasingly select, modify, and tailor their environments in part because of their genetic propensities, including genetically driven aspects of their personality, a concept known as *gene−environment correlation* (Plomin et al., 2013; Krapohl et al., 2014). In education, genetic factors not only influence children's aptitude and scholastic achievement, but also influence their appetite for learning.

The findings of the present study do not mean that teaching children to be grittier cannot be done or indeed that it is not beneficial. Throughout adult life, children will face challenges, thus perseverance in long-term goals might help them to develop habits of hard work and the continuous pursuit of their goals, despite the many obstacles they face. Our findings suggest, however, that although personality significantly predicts academic achievement, Grit adds little phenotypically or genetically to the prediction of academic achievement beyond well-established personality factors, especially Conscientiousness. Therefore, trying to increase Grit or perseverance could have long-term benefits for children but more research is warranted into intervention and training programs before concluding that such training increases educational achievement and life outcomes.

References

Boker, S., Neale, M., Maes, H., Wilde, M., Spiegel, M., Brick, T., . . . Fox, J. (2011). OpenMx: An open source extended structural equation modeling framework. *Psychometrika, 76,* 306–317. http://dx.doi.org/10.1007/s11336-010-9200-6

Briley, D. A., Domiteaux, M., & Tucker-Drob, E. M. (2014). Achievement-relevant personality: Relations with the Big Five and validation of an efficient instrument. *Learning and Individual Differences, 32,* 26–39. http://dx.doi.org/10.1016/j.lindif.2014.03.010

Chamorro-Premuzic, T., & Furnham, A. (2003). Personality predicts academic performance: Evidence from two longitudinal university samples. *Journal of Research in Personality, 37,* 319–338. http://dx.doi.org/10.1016/S0092-6566(02)00578-0

Chamorro-Premuzic, T., Harlaar, N., Greven, C. U., & Plomin, R. (2010). More than just IQ: A longitudinal examination of self-perceived abilities as predictors of academic performance in a large sample of UK twins. *Intelligence, 38,* 385–392. http://dx.doi.org/10.1016/j.intell.2010.05.002

Conard, M. A. (2006). Aptitude is not enough: How personality and behavior predict academic performance. *Journal of Research in Personality, 40,* 339–346. http://dx.doi.org/10.1016/j.jrp.2004.10.003

Duckworth, A. L. (2013). The key to success? Grit. *TED Talk*. Retrieved from http://www.ted.com/talks/angela_lee_duckworth_the_key_to_success_grit.html

Duckworth, A. L., & Eskreis-Winkler, L. (2013). True grit. *The Observer, 26,* 1–3.

Duckworth, A. L., & Gross, J. J. (2014). Self-control and grit: Related but separable determinants of success. *Current Directions in Psychological Science, 23,* 319–325. http://dx.doi.org/10.1177/0963721414541462

Duckworth, A. L., Peterson, C., Matthews, M. D., & Kelly, D. R. (2007). Grit: Perseverance and passion for long-term goals. *Journal of Personality and Social Psychology, 92,* 1087–1101. http://dx.doi.org/10.1037/0022-3514.92.6.1087

Duckworth, A. L., & Quinn, P. D. (2009). Development and validation of the Short Grit Scale (Grit-S). *Journal of Personality Assessment, 91,* 166–174. http://dx.doi.org/10.1080/00223890802634290

Duckworth, A. L., Quinn, P. D., & Tsukayama, E. (2012). What no child left behind leaves behind: The roles of IQ and self-control in predicting standardized achievement test scores and report card grades. *Journal of Educational Psychology, 104,* 439–451. http://dx.doi.org/10.1037/a0026280

Duckworth, A. L., Tsukayama, E., & Kirby, T. A. (2013). Is it really self-control? Examining the predictive power of the delay of gratification task. *Personality and Social Psychology Bulletin, 39,* 843–855. http://dx.doi.org/10.1177/0146167213482589

Eisenberg, N., Duckworth, A. L., Spinrad, T. L., & Valiente, C. (2014). Conscientiousness: Origins in childhood? *Developmental Psychology, 50,* 1331–1349. http://dx.doi.org/10.1037/a0030977

Eskreis-Winkler, L., Shulman, E. P., Beal, S. A., & Duckworth, A. L. (2014). The grit effect: Predicting retention in the military, the workplace, school and marriage. [Advance online publication]. *Frontiers in Psychology, 5,* 36. http://dx.doi.org/10.3389/fpsyg.2014.00036

Greven, C. U., Harlaar, N., Kovas, Y., Chamorro-Premuzic, T., & Plomin, R. (2009). More than just IQ: School achievement is predicted by self-perceived abilities—But for genetic rather than environmental reasons. *Psychological Science, 20,* 753–762. http://dx.doi.org/10.1111/j.1467-9280.2009.02366.x

Haworth, C. M. A., Davis, O. S. P., & Plomin, R. (2013). Twins Early Development Study (TEDS): A genetically sensitive investigation of cognitive and behavioral development from childhood to young adulthood. *Twin Research and Human Genetics, 16,* 117–125. http://dx.doi.org/10.1017/thg.2012.91

Kovas, Y., Haworth, C. M. A., Dale, P. S., & Plomin, R. (2007). The genetic and environmental origins of learning abilities and disabilities in the early school years. *Monographs of the Society for Research in Child Development, 72,* 1–144.

Krapohl, E., Rimfeld, K., Shakeshaft, N. G., Trzaskowski, M., McMillan, A., Pingault, J.-B., . . . Plomin, R. (2014). The high heritability of educational achievement reflects many genetically influenced traits, not just intelligence. *Proceedings of the National Academy of Sciences, USA of the United States of America, 111,* 15273–15278.

Laidra, K., Pullmann, H., & Allik, J. (2007). Personality and intelligence as predictors of academic achievement: A cross-sectional study from elementary to secondary school. *Personality and Individual Differences, 42,* 441–451. http://dx.doi.org/10.1016/j.paid.2006.08.001

Ligthart, L., & Boomsma, D. I. (2012). Causes of comorbidity: Pleiotropy or causality? Shared genetic and environmental influences on migraine and neuroticism. *Twin Research and Human Genetics, 15,* 158–165. http://dx.doi.org/10.1375/twin.15.2.158

Luciano, M., Wainwright, M. A., Wright, M. J., & Martin, N. G. (2006). The heritability of conscientiousness facets and their relationship to IQ and academic achievement. *Personality and Individual Differences, 40,* 1189–1199. http://dx.doi.org/10.1016/j.paid.2005.10.013

MacCann, C., Duckworth, A. L., & Roberts, R. D. (2009). Empirical identification of the major facets of conscientiousness. *Learning and Individual Differences, 19,* 451–458. http://dx.doi.org/10.1016/j.lindif.2009.03.007

McCabe, K. O., Van Yperen, N. W., Elliot, A. J., & Verbraak, M. (2013). Big Five personality profiles of context-specific achievement goals. *Journal of Research in Personality, 47,* 698–707. http://dx.doi.org/10.1016/j.jrp.2013.06.003

Moffitt, T. E., Arseneault, L., Belsky, D., Dickson, N., Hancox, R. J., Harrington, H., . . . Caspi, A. (2011). A gradient of childhood self-control predicts health, wealth, and public safety. *Proceedings of the National Academy of Sciences, USA of the United States of America, 108,* 2693–2698. http://dx.doi.org/10.1073/pnas.1010076108

Mullins-Sweatt, S. N., Jamerson, J. E., Samuel, D. B., Olson, D. R., & Widiger, T. A. (2006). Psychometric properties of an abbreviated instrument of the five-factor model. *Assessment, 13,* 119–137. http://dx.doi.org/10.1177/1073191106286748

Noftle, E. E., & Robins, R. W. (2007). Personality predictors of academic outcomes: Big Five correlates of GPA and SAT scores. *Journal of Personality and Social Psychology, 93,* 116–130. http://dx.doi.org/10.1037/0022-3514.93.1.116

Paunonen, S. V., Haddock, G., Forsterling, F., & Keinonen, M. (2003). Broad versus narrow personality measures and the prediction of behaviour across cultures. *European Journal of Personality, 17,* 413–433. http://dx.doi.org/10.1002/per.496

Paunonen, S. V., & Jackson, D. N. (2000). What is beyond the Big Five? Plenty! *Journal of Personality, 68,* 821–835. http://dx.doi.org/10.1111/1467-6494.00117

Plomin, R., DeFries, J. C., Knopik, V. S., & Neiderhiser, J. M. (2013). *Behavioral genetics* (6th ed.). New York, NY: Worth Publishers.

Poropat, A. E. (2009). A meta-analysis of the five-factor model of personality and academic performance. *Psychological Bulletin, 135,* 322–338. http://dx.doi.org/10.1037/a0014996

Price, T. S., Freeman, B., Craig, I., Petrill, S. A., Ebersole, L., & Plomin, R. (2000). Infant zygosity can be assigned by parental report questionnaire data. *Twin Research, 3,* 129–133. http://dx.doi.org/10.1375/136905200320565391

Richardson, M., Abraham, C., & Bond, R. (2012). Psychological correlates of university students' academic performance: A systematic review and meta-analysis. *Psychological Bulletin, 138,* 353–387. http://dx.doi.org/10.1037/a0026838

Rijsdijk, F. V., & Sham, P. C. (2002). Analytic approaches to twin data using structural equation models. *Briefings in Bioinformatics, 3,* 119–133. http://dx.doi.org/10.1093/bib/3.2.119

Samuel, D. B., Mullins-Sweatt, S. N., & Widiger, T. A. (2013). An investigation of the factor structure and convergent and discriminant validity of the five-factor model rating form. *Assessment, 20,* 24–35. http://dx.doi.org/10.1177/1073191112455455

Shechtman, N., DeBarger, A. H., Dornsife, C., Rosier, S., & Yarnall, L. (2013). *Promoting grit, tenacity, and perseverance: Critical factors for success in the 21st century*. Washington, DC: U.S. Department of Education.

Tangney, J. P., Baumeister, R. F., & Boone, A. L. (2004). High self-control predicts good adjustment, less pathology, better grades, and interpersonal success. *Journal of Personality, 72,* 271–324. http://dx.doi.org/10.1111/j.0022-3506.2004.00263.x

Trapmann, S., Hell, B., Hirn, J.-O. W., & Schuler, H. (2007). Meta-analysis of the relationship between the Big Five and academic success at University. *Zeitschrift Für Psychologie. The Journal of Psychology, 215,* 132–151.

Turkheimer, E., Pettersson, E., & Horn, E. E. (2013). A phenotypic null hypothesis for the genetics of personality, *Annual Review of Psychology, 65,* 515–540. http://dx.doi.org/10.1146/annurev-psych-113011-143752

Vedel, A. (2014). The Big Five and tertiary academic performance: A systematic review and meta-analysis. *Personality and Individual Differences, 71,* 66–76. http://dx.doi.org/10.1016/j.paid.2014.07.011

Von Culin, K. R., Tsukayama, E., & Duckworth, A. L. (2014). Unpacking grit: Motivational correlates of perseverance and passion for long-term goals. *The Journal of Positive Psychology, 9,* 306–312. http://dx.doi.org/10.1080/17439760.2014.898320

von Stumm, S., Hell, B., & Chamorro-Premuzic, T. (2011). The hungry mind: Intellectual curiosity is the third pillar of academic performance. *Perspectives on Psychological Science, 6,* 574–588. http://dx.doi.org/10.1177/1745691611421204

Wagerman, S. A., & Funder, D. C. (2007). Acquaintance reports of personality and academic achievement: A case for conscientiousness. *Journal of Research in Personality, 41,* 221–229. http://dx.doi.org/10.1016/j.jrp.2006.03.001

Zimmerman, B. J., Bandura, A., & Martinez-Pons, M. (1992). Self-motivation for academic attainment: The role of self-efficacy beliefs and personal goal setting. *American Educational Research Journal, 29,* 663–676. http://dx.doi.org/10.3102/00028312029003663

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Chapter 6: Genetics affects choice of academic subjects as well as achievement

This chapter, studying how genetics affects the subject choice after compulsory education and educational achievement in those chosen subjects, is presented as a published paper. It is an exact copy of this publication.

Rimfeld, K., Ayorech, Z., Dale, P. S., Kovas, Y., & Plomin, R. (2016). Genetics affects choice of academic subjects as well as achievement. *Scientific reports*, *6*.

Supplementary materials for this chapter, as detailed in the text, are attached in Appendix 4.

Genetics affects choice of academic subjects as well as achievement

Kaili Rimfeld[1], Ziada Ayorech[1], Philip S. Dale[2], Yulia Kovas[1,3,4] & Robert Plomin[1]

We have previously shown that individual differences in educational achievement are highly heritable throughout compulsory education. After completing compulsory education at age 16, students in England can choose to continue to study for two years (A-levels) in preparation for applying to university and they can freely choose which subjects to study. Here, for the first time, we show that choosing to do A-levels and the choice of subjects show substantial genetic influence, as does performance after two years studying the chosen subjects. Using a UK-representative sample of 6584 twin pairs, heritability estimates were 44% for choosing to do A-levels and 52–80% for choice of subject. Achievement after two years was also highly heritable (35–76%). The findings that DNA differences substantially affect differences in appetites as well as aptitudes suggest a genetic way of thinking about education in which individuals actively create their own educational experiences in part based on their genetic propensities.

Educational achievement is a strong predictor of many life outcomes, such as higher education, occupation, health and even life expectancy[1–3]. Because differences in children's educational achievement and the subject choices they make in secondary school will propel young individuals on to a variety of lifelong trajectories, it is important to understand what influences the subject choices students take after compulsory education and to understand why students differ so widely in school grades. Subject choice after compulsory education is especially important as all academic learning after the age of 16 in England and Wales is considered to be preparation for further education and university entry.

Educational achievement has been studied using quantitative genetic methods, such as the classical twin method that compares identical twins to non-identical twins, to estimate the extent to which individual differences in school achievement are influenced by genetic factors and shared or non-shared environmental factors. Shared environmental factors that contribute to the similarities between siblings raised in the same family[4], for example home or school environment, are certainly important, as children have to be taught skills such as reading and writing, they have to gain knowledge of scientific theories and historical facts, and they need guidance to appreciate music and art. Nonetheless, children from the same home, attending the same school and even the same classroom differ in academic performance, indicating that other factors besides shared environmental factors must be present. Previous research has shown that educational achievement is substantially heritable from the early school years until the end of compulsory education, which means that, to a large extent, differences in children's educational achievement can be explained by inherited differences in children's DNA sequence[5–9]. It is reasonable to assume that this high heritability of educational achievement is explained by children's aptitude, or intelligence, but we have shown that educational achievement in the early school years is even more heritable than intelligence[10]. Furthermore, our recent studies have shown that the high heritability of educational achievement at the end of compulsory education is not explained by intelligence alone, but rather is influenced by a constellation of genetically related traits, such as self-efficacy, behavioral problems, and personality[11,12].

Previous research demonstrates that genetic differences between children not only influence how well they perform at school, but also how easy or enjoyable they find learning in general[13,14]. It is also noteworthy that children may find certain subjects more enjoyable than others even when their achievement is good across subjects[11,14]. We hypothesize that given a choice, children will select, modify and create their own educational experiences in part based on their genetic propensities, a concept known as genotype-environment correlation[15]. These findings suggest that children are not passive recipients of instruction, but instead are active participants in their path to

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knowledge. In a more personalized education system, children would choose educational subjects early allowing them to focus on their strengths and interests. However, until the age of 16, students in England and Wales have little choice. At age 14 when they start their GCSE (General Certificate of Secondary Education) course, students are given some choice; however, English, mathematics and sciences are compulsory subjects for GCSE, and some schools require students to take separate science courses (biology, physics and chemistry), as compared to a combined science course. Many schools also require students to take English literature and at least one modern foreign language course, while others restrict them to only one foreign language course. Although students typically take 10 GCSE subjects, the differences in requirements across schools interferes with the investigation of student choices. For these reasons we were previously unable to investigate genetic influence on subject choice.

At age 16, after compulsory education, it is possible to study choice. Students can choose to study towards the A-levels (General Certificate of Education Advanced Level), a two-year course, which is a prerequisite for higher education. For the first time in their educational experience, students are free to choose all of their A-level subjects from over 80 different options, typically choosing three to four A-level courses. However, despite the importance of choosing to do A-levels and subject choices, it is largely unknown why children differ in such choices and what influences their decisions. Because their A-level grades are used for university admission, it is reasonable to assume that children choose subjects in which they expect to do well or choose the subjects they enjoy, as they are required to focus and put substantial effort in these disciplines during the two A-level years. The focus of the current study is to investigate the extent to which students' choice to do A-levels and their choice of A-level subjects as well as subsequent achievement can be explained by genetic or environmental influences.

The current study

The study used a large UK-representative twin sample, the Twins Early Development Study (TEDS)[16], to investigate the genetic and environmental contributions in choosing to do A-levels and subject choice at age 16, as well as achievement in the chosen subjects at age 18. Based on previous research, we hypothesized that the heritability of school achievement at age 18 would be substantial, and that it would be substantial across the multiple subjects children study at school after compulsory education. We also investigated, for the first time, the extent to which the decision to continue studying at A-level and the students' subject choice is made on the basis of their genetic propensities. The design also estimates the influence of shared environmental factors that reflect shared school and family influences and non-shared environment such as child-specific school recommendations and parental advice for choosing to do A-levels and for choosing specific subjects.

Results

Descriptive statistics. Table 1 presents the proportion of students taking A-level and their subject choices for the whole sample, for boys and girls separately, and for each of the five zygosity groups: MZ males, MZ females, DZ males, DZ females and DZ opposite-sex twin pairs. Using the TEDS data collected at age 18, we show that about 50% of the participants (6613 students from the overall sample of 13,168, of whom 7012 were female and 6156 were male) choose to continue their studies at A-level, which is similar to the UK national average (42% of students in the 16–18 year cohort in England and Wales continue to do A-levels: https://www.gov.uk/government/uploads/system/uploads/attachment_data/file/502158/SFR03_2016__A_level_and_other_level_3_results_in_England_SFR_revised.pdf) . There were significant differences between girls and boys for choosing to do A-levels; 57% of females chose to study at A-level compared to 43% of males. Overall, girls and boys choose STEM subjects in equal proportions (49% girls, 51% boys), although girls much prefer biology (63% girls, 37% boys) and boys much prefer physics (23% girls, 77% boys). Boys slightly prefer mathematics (42% girls, 58% boys); there is little difference in chemistry (48% girls, 52% boys). Girls more often chose humanities subjects (58% girls, 42% boys), especially English (73% girls, 27% boys), second language (68% girls, 32% boys), and psychology (77% girls, 23% boys).

Although there are substantial sex differences in choice of A-level subjects, Table 2 shows that girls and boys do not differ much in their A-level exam results at age 18. Significant sex differences were found only for the overall A-level grade, humanities composite, and psychology; however, these mean differences were not substantial. ANOVA results show that sex and zygosity explain less than 1% of variance in A-level results except for psychology where they explain 5% of the variance. For the subsequent analyses the data were corrected for the small mean sex and zygosity differences, as described in the Methods section.

Twin analyses. We investigated quantitative and qualitative sex differences using the full sex-limitation model, as described in the Methods section. No significant qualitative sex differences emerged. Although some significant quantitative sex differences emerged for overall A-level grade, mathematics, chemistry, history and humanities, the differences were small. (Full model fit statistics with the nested models are presented in Supplementary Table 1; ACE estimates and confidence intervals for males and females are listed in Supplementary Table 2.). For example, for A-level mean grade, heritability was 52% (95% CI: 0.38; 0.69) for girls and 57% (95% CI 0.36; 0.69) for boys. The largest difference in heritability was for mathematics 70% (95% CI 0.34; 0.77) girls, and 51% (95% CI 0.15; 0.67); the overlapping confidence intervals for these estimates warrant little confidence because the analysis is underpowered in that only 15% of the sample chose mathematics; the sample was then further reduced by comparing gender as well as zygosity (this is evident by the wide confidence intervals around estimates when calculated for males and females separately). For these reasons, and to increase power in the present analyses, the full sample was used, combining males and females and including opposite-sex pairs.

We used the liability threshold model to calculate ACE estimates for choosing to study at A-level and A-level subject choice, as described in the Methods section. As illustrated in Fig. 1, choosing to do A-levels was moderately heritable (44%) and the influence of shared environment was just as large (47%). In contrast, the subjects students chose at A-level were more heritable (50–80%) and much less influenced by shared environment

Subject	N*	Male	Female	X^2	MZm	DZm	MZf	DZf	DZos
A-level choice	6613	2826	3787	40.60**	928	934	1428	1197	2126
	(50%)	(43%)	(57%)		(14%)	(14%)	(22%)	(18%)	(32%)
Humanities choice	2561	1068	1493	12.57**	341	345	573	452	850
	(19%)	(42%)	(58%)		(13%)	(14%)	(22%)	(18%)	(33%)
STEM choice	3417	1740	1677	18.57**	573	584	660	539	1061
	(26%)	(51%)	(49%)		(17%)	(17%)	(19%)	(16%)	(31%)
Mathematics choice	1988	1147	841	66.93**	370	371	344	260	643
	(15%)	(58%)	(42%)		(18%)	(19%)	(17%)	(13%)	(32%)
Biology choice	1634	603	1031	36.53**	204	213	374	352	491
	(12%)	(37%)	(63%)		(13%)	(13%)	(23%)	(22%)	(30%)
Physics choice	846	652	194	188.94**	212	220	79	67	268
	(6%)	(77%)	(23%)		(25%)	(26%)	(9%)	(8%)	(32%)
Chemistry choice	1276	608	668	0.73	214	204	236	231	391
	(10%)	(48%)	(52%)		(17%)	(16%)	(19%)	(18%)	(31%)
English composite choice	1807	490	1317	174.43**	164	155	471	414	603
	(14%)	(27%)	(73%)		(9%)	(9%)	(26%)	(23%)	(33%)
Second language choice	544	174	370	28.55**	48	55	166	111	164
	(4%)	(32%)	(68%)		(8%)	(10%)	(31%)	(20%)	(30%)
History choice	1291	571	720	4.54*	178	169	288	211	445
	(10%)	(44%)	(56%)		(14%)	(13%)	(22%)	(16%)	(35%)
Geography choice	1032	466	566	0.01	146	159	217	92	325
	(8%)	(55%)	(45%)		(14%)	(15%)	(21%)	(18%)	(32%)
Psychology choice	1222	285	937	139.37**	107	94	355	267	399
	(9%)	(23%)	(77%)		(9%)	(8%)	(29%)	(22%)	(33%)
Total	13, 168								

Table 1. Proportion of the sample choosing to progress to A-level and proportion of participants choosing an A-level subject. N sample size after exclusions (individuals), proportions of across gender and zygosity groups reported as a proportion of students who chose the subject; MZ monozygotic; DZ dizygotic; m male; f female; os opposite sex; X^2 Chi-square results comparing choice between males and females (one randomly selected twin per pair); *p 0.05; **p 0.01.

(0–23%). (Twin tetrachoric correlations and full-model fit statistics with confidence intervals are presented in Supplementary Table 3.).

Figure 2 presents ACE estimates for academic achievement at age 18. A-level mean performance was highly heritable (59%) with only a small proportion of the variance explained by shared environmental factors (7%). Heritability was non-significantly lower for the humanities composite (49%) compared to STEM (65%). Although heritabilities differed across subjects from 35% for history to 76% for chemistry, the sample size was too small to provide adequate power to detect such differences, which can be seen in the estimates' overlapping confidence intervals. (Full-model fit statistics with confidence intervals are presented in Supplementary Table 4.).

Discussion

These results show, for the first time, that genetic factors influence academic choice, not just achievement. Whether or not 16-year-olds choose to continue their studies at A-level in preparation for university is influenced in equal measure by genetic (44%) and shared environmental factors (47%). Choosing specific A-level subjects is more heritable (50% for humanities, 60% for STEM) and less influenced by shared environment (18% for humanities, 23% for STEM). Genetic factors affect subject choice across a wide range of school subjects, including second language learning, mathematics and psychology. We could not repeat the analyses across all A-level subjects because some subjects were chosen by very few students. For example, it would have been interesting to study the etiology of subject choice for more art-related subjects, such as art, drama and music, but it was not possible in the present study because of limited power.

How can DNA differences affect choice? Two obvious possibilities are previous achievement and ability. That is, it seems reasonable to expect that students make A-level choices in part on the basis of previous educational achievement, which is substantially heritable. It is also possible that general intelligence, which is also substantially heritable, contributes to these choices independently from previous achievement. We are currently investigating the role of earlier achievement and ability, but we are especially interested in the less obvious possibility that choice is governed by appetites as well as by achievement and ability. In other words, it seems likely that students choose subjects they enjoy, and this could be a cause rather than just an effect of their previous achievement. Our ongoing research capitalizes on the longitudinal data available from this sample to explore the motivational antecedents of choice. Our future research plans also include using all the data collected in TEDS longitudinally to study the early and concurrent predictors and correlates of educational achievement and subject choice at A-levels.

Subject	N	Whole sample	Male	Female	MZm	DZm	MZf	DZf	DZos	Sex	Zyg	Sex x Zyg	R^2
A-level mean grade	3053	3.90	3.85	3.94	3.82	3.84	3.97	3.89	3.93	4.87*	0.04	1.62	<0.01
		(1.16)	(1.20)	(1.13)	(1.24)	(1.23)	(1.10)	(1.19)	(1.12)				
Humanities mean grade	1280	4.00	3.90	4.07	3.82	3.99	4.11	4.03	3.99	6.84**	0.01	1.91	<0.01
		(1.14)	(1.18)	(1.10)	(1.18)	(1.20)	(1.12)	(1.10)	(1.12)				
STEM mean grade	1723	3.89	3.85	3.92	3.80	3.84	3.92	3.9	3.93	1.01	0.27	0.57	<0.01
		(1.31)	(1.32)	(1.31)	(1.36)	(1.35)	(1.28)	(1.38)	(1.25)				
Mathematics mean grade	1012	4.34	4.27	4.43	4.20	4.27	4.39	4.50	4.37	3.63	0.84	1.33	<0.01
		(1.28)	(1.33)	(1.20)	(1.43)	(1.35)	(1.25)	(1.16)	(1.19)				
Biology grade	812	3.95	3.91	3.98	3.74	4.11	3.87	4.02	3.98	0.53	3.45	1.15	<0.01
		(1.39)	(1.34)	(1.42)	(1.30)	(1.33)	(1.36)	(1.48)	(1.40)				
Physics grade	443	3.97	3.96	4.20	4.07	3.79	4.09	3.79	4.06	0.15	1.20	0.97	<0.01
		(1.38)	(1.38)	1.28	(1.32)	(1.45)	(1.36)	(1.60)	(1.33)				
Chemistry grade	646	4.13	4.05	4.20	3.89	4.23	4.21	4.22	4.12	2.06	1.34	1.33	<0.01
		(1.30)	(1.32)	(1.28)	(1.38)	(1.37)	(1.27)	(1.27)	(1.26)				
English composite grade	904	4.01	4.09	3.98	4.01	4.16	4.08	3.91	3.98	1.50	0.91	0.90	<0.01
		(1.19)	(1.24)	(1.17)	(1.22)	(1.27)	(1.19)	(1.21)	(1.15)				
Second language mean grade	275	4.11	4.15	4.09	4.33	3.90	4.11	4.30	3.96	0.19	0.51	1.20	<0.01
		(1.14)	(1.21)	(1.11)	(1.27)	(1.20)	(0.94)	(1.13)	(1.27)				
History grade	677	4.11	4.06	4.16	4.07	4.1	4.12	4.18	4.1	1.15	0.04	0.13	<0.01
		(1.17)	(1.23)	(1.12)	(1.19)	(1.25)	(1.19)	(1.11)	(1.15)				
Geography grade	496	4	3.91	4.08	3.79	3.97	4.25	3.93	3.99	2.60	0.61	1.97	<0.01
		(1.15)	(1.19)	(1.1)	(1.22)	(1.20)	(1.09)	(1.16)	(1.10)				
Psychology grade	600	3.66	3.31	3.77	3.52	3.45	3.94	3.78	3.44	15.01**	7.07**	4.50**	0.05
		(1.25)	(1.14)	(1.27)	(1.13)	(1.11)	(1.18)	(1.25)	(1.33)				

Table 2. Mean scores and (standard deviations) for A-level exam results. Scores for subject means have a maximum grade of 6 and a minimum of 1, representing grades A* to E. N = sample size after exclusions; MZ = monozygotic; DZ = dizygotic; m = male; f = female; os = opposite sex. ANOVA analyses (one randomly-selected twin per pair) tested the effect of sex and zygosity: results = F statistic; *$p < 0.05$; **$p < 0.01$; R^2 = proportion of variance explained by sex, zygosity and their interaction.

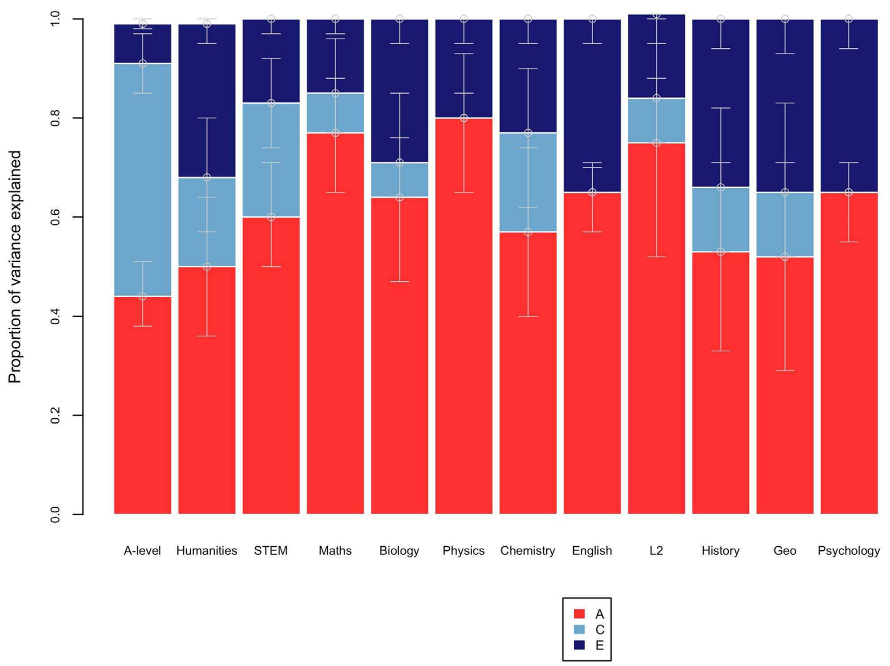

Figure 1. Genetic and environmental estimates for A-level choice and choice of A-level subjects. Liability threhold model-fitting results (error bars representing the 95% confidence intervals). A = additive genetic, C = shared environmental and E = non-shared environmental components of variance. STEM = science, technology, engineering and mathematics, Geo = geography, L2 = second language

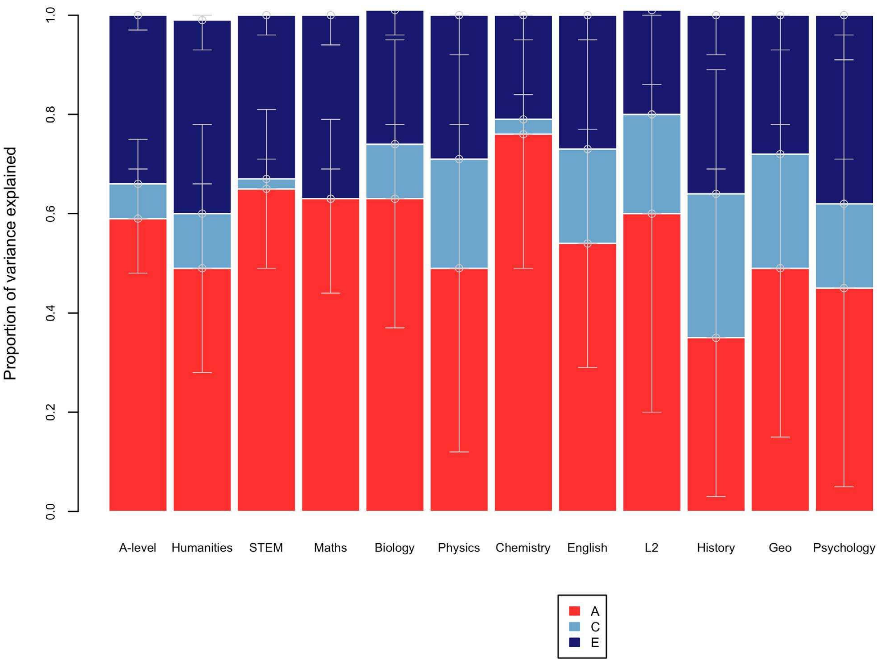

Figure 2. Genetic and environmental estimates for A-level exam results: univariate model-fitting results (error bars representing the 95% confidence intervals). A = additive genetic, C = shared environmental and E = non-shared environmental components of variance. STEM = science, technology, engineering and mathematics, Geo = geography, L2 = second language.

Another noteworthy aspect of the results in relation to choice is the substantial influence of shared environment on choosing to do two years of A-level studies. We found that nearly half (47%) of the liability to make this choice can be attributed to shared environment. Although it does not seem surprising that parents and teachers influence both members of a twin pair to make similar choices about whether to do A-levels, this finding is noteworthy because, despite its reasonableness, it is rare to find such a major role for shared environment for other traits. It is possible that teachers and parents encourage both children in a twin pair to continue their studies at A-levels, but that specific career advice is more personalized. As noted above, shared environment has only half as much impact on choice of A-level subjects (23% for STEM; 18% for humanities), and it has even less effect on A-level grades (2% for STEM; 11% for humanities). We are using the longitudinal data from TEDS to investigate the specific aspects of the shared environment that influence A-level choice and to explore why these same environmental factors have less of an influence on specific subject choice and achievement.

Finding substantial heritability for A-level exam scores at age 18 (65% for STEM; 49% for humanities) is consistent with our earlier research showing that educational achievement is highly heritable across compulsory education[5,6,11,12]. Nonetheless, this finding is remarkable because only half the population chooses to do A-levels, both in TEDS and in the UK (https://www.gov.uk/government/uploads/system/uploads/attachment_data/file/207749/Main_text_-_SFR19_2013.pdf). This self-selection leads to a restriction of range of ability among these university-bound students. Despite this restriction of range, DNA differences continue to differentiate performance on A-level exams to a similar extent as achievement during earlier years when education was compulsory for all children.

Although it has been said many times, it is worth reiterating that heritability does not imply immutability. Heritability describes the extent to which phenotypic differences between individuals can be explained by genetic differences in a particular population with that population's mix of genetic and environmental influences at that time. Therefore, the findings of the current study may not generalize to other populations. In other words, heritability describes what is, not what could be. High heritability of educational achievement does not doom attempts to have all children reach a minimal level of literacy or numeracy. In the same way, finding that shared environmental influence is modest for A-level achievement does not mean that schools or teachers are unimportant. Instead, these results indicate that children's educational potential could be maximized if environments were more personalized and suited to their specific needs. We hope that the findings of the present study will lead to further research in other populations to advance understanding of educational choices and achievement throughout school years and beyond.

Our findings imply that inherited differences in DNA sequence are associated with academic choice and achievement. Nothing would advance research in this area more than identifying the specific DNA sequences responsible for heritability. This is beginning to happen, for example, for educational attainment[17] and for general intelligence[18]. However, the main finding to date across the life sciences is that the heritability of complex traits and common disorders is due to many, perhaps thousands, of DNA differences, each of very small effect size. Indeed, the largest effect size for educational attainment (years of schooling) is an association that accounts for a mere 0.02% of the variance in a genome-wide association meta-analysis with a sample of 120,000[17]. Rather than focusing on a handful of such DNA differences that reach genome-wide statistical significance, researchers are beginning to use polygenic scores that aggregate thousands of DNA differences[19]. Even so, the missing heritability gap is large; for example, for educational attainment, a polygenic score obtained from a recent genome-wide association meta-analysis of educational attainment with nearly 300,000 adults accounted for about 5% of the variability for educational attainment in independent samples, even though this variable is about 50% heritable[20]. Nonetheless, we have shown in our sample that this polygenic score for educational attainment in adults is significantly associated with educational achievement and general intelligence in 16-year-olds[21]. In our future research, we will use this polygenic score and other polygenic scores (together with the SNP-based methods) to investigate academic choice and achievement at A-levels. Polygenic scores are needed that are derived from bigger and better genome-wide association studies – that is, with bigger samples that can detect even smaller effects and with better measures of educational achievement rather than the proxy measure of educational attainment.

Finding substantial genetic influence on choice as well as achievement supports a genetic way of thinking about education in which individuals actively choose and create educational experiences on the basis of their genetic propensities, called *genotype-environment correlation*[22]. This active view of education ('leading out') contrasts with the traditional passive model of instruction ('shoving in'). Giving children a more active choice in their curricula would allow children to become more active participants in their education rather than passive receivers of instruction. Finding genetic influence on choice as well as achievement does not dictate any specific policies, but it supports educational trends away from a one-size-fits-all curriculum towards providing more opportunities, choice and personalized learning, helping each child to reach their maximum potential.

Method

Participants. The sample was drawn from the Twins Early Developmental Study (TEDS), a representative sample of twins born in England and Wales between 1994 and 1996. Of the 16,000 twin pairs originally recruited, over 10,000 remain actively involved in TEDS. Their recruitment and representativeness has been described in detail elsewhere[5,23]. The present study included all individuals with educational achievement data available at 18. Participants with severe medical or psychiatric problems or whose mothers had severe medical complications during pregnancy were excluded from the analysis. We also excluded participants with unknown zygosity. Zygosity was assessed by a parent-reported questionnaire of physical similarity, which is over 95% accurate when compared to DNA testing[24]. For cases where zygosity was unclear from this questionnaire, DNA testing was conducted. After exclusions, the total number of individuals for whom data at 18 were available was 13,226 individuals (6584 twin pairs), of whom 2318 were monozygotic (MZ) twin pairs, 2146 were dizygotic same-sex pairs (DZss) and 2120 were dizygotic opposite-sex (DZos) pairs. A-level exam achievement results were available for half of the participants (the proportion of participants who took the A-level exams): 3308 twin pairs of which 1178 were MZ twin pairs, 1067 were DZ same-sex twin pairs, and 1063 were DZ opposite-sex twin pairs.

In the twin method, DZ twin pairs are needed to delineate genetic and environmental contributions to a trait, with same-sex DZ twins most often used because they provide a more appropriate control for MZ twin pairs, who are always the same sex[4,25]. When data are available from opposite-sex twin pairs, sex differences in the etiology of individual differences can also be explored. Sex limitation results are reported in the Results section. Because little evidence was found for significant sex differences for the achievement data and to increase power, we used the full sample, including opposite-sex twin pairs.

Measures. The TEDS sample has now completed compulsory education. In England and Wales, compulsory education ends with the General Certificate of Secondary Education (GCSE), a standardized examination typically taken at the age of 16. Completion of GCSE examinations marks a unique stage for pupils who are now, for the first time, free to choose whether to leave formal education or to continue their studies to complete further education (FE). In the UK, FE refers to courses offered in separate FE colleges or more commonly, available within the sixth-form part of a school, which are distinct from the undergraduate and graduate degrees typically offered at universities (http://www.cambridgeassessment.org.uk/Images/140668-popularity-of-a-level-subjects-among-uk-university-students.pdf). These FE qualifications are commonly taken over a two-year period, with official examinations held at the end of each year, leading to a formal qualification known as the General Certificate of Education Advanced level, or A-level, which is the focus of the present study. Alternative qualifications including the International Baccalaureate, NVQ (National Vocational Qualification) and BTEC (Business and Technology Education Council) are also considered FE but were not analyzed in the present study (https://www.studential.com/further-education/vocational-qualifications).

Unlike in previous school years, at A-level pupils are free to choose all of their courses from over 80 different subjects, typically choosing three to four subjects studied during the two-year period (http://www.cambridgeassessment.org.uk/Images/140668-popularity-of-a-level-subjects-among-uk-university-students.pdf). Grades achieved in both exams (GCSE and A-level) are converted into a points-based system (https://www.ucas.com/ucas/undergraduate/getting-started/entry-requirements/tariff), which is evaluated by the student's chosen university along with previous school performance and teacher-predicted results, as criteria for university entry. However, some universities evaluate specific grades achieved, not just achievement based on the overall points-based system. A detailed description of the UK education system can be found on UK Department of Education website (https://www.gov.uk/government/uploads/system/uploads/attachment_data/file/219167/v01-2012ukes.pdf).

A questionnaire, designed to obtain A-level and other post-16 qualifications as well as work destinations, was sent to all TEDS families at the end of the academic school year when twins reached age 18. The full questionnaire was completed either by twins themselves or by their parents. We have previously shown that self-reported exam results are accurate[12]. For GCSE (General Certificate of Secondary Education) exam results that children take at the age of 16 the grades were verified using the National Pupil Database (NPD; https://www.gov.uk/government/uploads/system/uploads/attachment_data/file/251184/SFR40_2013_FINALv2.pdf) using the sample of 7367 twins, yielding a correlation of 0.99 for mathematics, 0.98 for English and 0.95 for all the sciences.

A-level examination grades (ranging from A* to E) were obtained for each twin and were coded from 6(A*) to 1(E) to ensure equivalent numerical comparisons. Because no subjects at A-level are compulsory and the range of subjects chosen is so wide, the sample sizes were too small to provide adequate power for analyses of separate subjects except for biology, chemistry, physics, history, geography and psychology. For this reason and to increase power generally, we created a composite STEM variable (science, technology, engineering and mathematics), which was derived as a mean grade of all sciences (mean of science, biology, chemistry and physics grades), technology (mean of technology and information communications technology grades), engineering (mean of engineering and mechanical engineering grades), and mathematics (mean of any core mathematics and further mathematics grades) courses. Composites were also created for English (mean of any English language and English literature grades), second language (mean of any second language course grade), and humanities (mean of history, religious studies, media studies and geography grades). An A-level mean grade, computed as the average grade achieved across all subjects in the dataset, was also created to ensure even those subjects with sample sizes too small to be considered separately were included in the analysis. In order to assess individual differences in subject choice we created categorical variables indicating whether or not pupils chose to take the individual or composite subjects described above. Finally, we created a categorical A-level choice variable to indicate whether or not participants chose to do their A-levels.

Analyses. The data were described in terms of means and variance comparing boys with girls and MZ and DZ twins. Analysis of variance (ANOVA) was then used to explore sex and zygosity differences in means and variances and their interaction, for A-level grades. For subsequent analyses the achievement scores were corrected for small age and sex differences using the regression method because MZ twins are always the same sex, along with the mean effect of age, which is perfectly correlated across pairs, both factors which if uncorrected would inflate estimates of shared environmental influence[26]. Standardized age and sex corrected residuals were used for all subsequent analyses. Finally, prior to conducting twin analyses, the data were corrected for normality using the rank-based van der Waerden transformation[27,28]. Corrections were performed because achievement data were slightly positively skewed, showing a ceiling effect similar to data achieved from UK national statistics (https://www.gov.uk/government/uploads/system/uploads/attachment_data/file/365986/SFR42_2014_provisional__A_level_and_level_3_SFR.pdf).

Twin analyses. In order to investigate the relative genetic and environmental contribution to individual differences in educational achievement, we used the twin design, a quantitative genetic method which exploits the known coefficients of relatedness between identical (MZ) and non-identical (DZ) twins, to apportion phenotypic variance into additive genetic (A), shared environmental (C) and non-shared or unique environmental (E) components. Genetic effects are perfectly correlated for MZ twin pairs who are 100% genetically similar compared to DZ twin pairs who, like non-twin siblings, share 50% of the segregating genes. Shared environmental effects are perfectly correlated for MZ and DZ twin pairs reared together while non-shared environmental effects are uncorrelated for members of a twin pair and do not contribute to similarities between twins. Based on these known relations and the standard quantitative genetic model (Falconer's formula), heritability (A) can be roughly estimated by doubling the difference between MZ and DZ twin correlations. The residual familial resemblance not explained by heritability is accounted for by the C component, calculated by subtracting the heritability estimate from the MZ correlation. The E component represents the remaining variance and measurement error and is calculated by deducting the A and C components from unity, as the total variance cannot exceed 100%[4,25].

The ACE parameters can be estimated more accurately using structural equation model fitting with maximum-likelihood estimation, which also provides 95% confidence intervals and formal model fit statistics. The structural equation modeling program OpenMx was used for all model fitting analyses[29].

Power was calculated using Genepi Twin Power calculator[30,31], which shows that the analyses had over 80% power for both the subject choice and achievement variables. The analyses had less than 80% power to detect C in specific subject achievement grades of second language, geography and psychology as is evident from the large confidence intervals around the estimates, but were reported for completeness.

Sex-limitation model. When data are available for both same sex DZ twin pairs and opposite-sex DZ twins, the standard univariate ACE model can be extended to a sex-limitation model to test the differences in the etiology of the trait of interest by comparing twin correlations across five zygosity groups: MZ males, MZ females, DZ males, DZ females and DZ opposite-sex twin pairs[4,32]. Quantitative sex differences refer to sex differences in the magnitude of ACE estimates. Qualitative sex differences test whether there are different genetic or different environmental factors influencing boys and girls separately, which is largely based on whether DZ same-sex twin correlations are higher than DZ opposite-sex correlations[32].

The sex-limitation model was analyzed using the structural equation program OpenMx by fitting a series of nested models and testing the relative fit of the models[29]. In the full model, all parameters are allowed to vary across all five zygosity groups (genetic correlation between DZos, ACE estimates, variances, ACE estimates, DZss and DZos variances and correlations). To test for qualitative sex differences, the genetic or shared environmental correlation is constrained to expected values (1.0 or 0.5 respectively), while other estimates are allowed to vary in the model. Quantitative genetic differences are tested by a reduced model in which ACE estimates are equated for males and females and the DZos genetic correlation is constrained to 0.5. The sex-limitation model is described in more detail elsewhere[4,6,32].

Liability threshold model. Because subject choice was measured as a dichotomous trait (choosing a subject or not), twin resemblance was assessed by concordances between MZ and DZ twins by comparing the twin who took an A-level course, to their co-twin. Concordance represents an index of risk, often encountered when assessing the presence or absence of a disease; but is used in the present study as the presence or absence of subject choice[4,25]. Analyses of categorical twin data assume that observed categories represent an imprecise measurement of an underlying normal distribution of liability[25]. The degree of agreement between MZ twin pairs who are genetically 100% similar is then compared to the degree of agreement between DZ twin pairs, who share 50% of their segregating genes on average using the correlation of liability (tetrachoric correlation). The liability threshold model is described in detail elsewhere[25]. The structural equation program OpenMX was used for the liability threshold model[29].

References

1. Bronfenbrenner, U., Mcclelland, P. D., Stephen, C., Moen, P. & Wethington, E. *e State of Americans: is Generation and the Next*. (Simon and Schuster, New York, 1996).
2. Cutler, D. M. & Lleras-Muney, A. Education and health: insights from international comparisons. No.w17738. *NBE Wor . Pap*. (2012).
3. Arendt, J. N. Does education cause better health? A panel data analysis using school reforms for identification. *Econ. Educ. ev.* **24,** 149–160 (2005).
4. Plomin, R., DeFries, J. C., Knopik, V. S. & Neiderhiser, J. M. *Behavioral Genetics.* 6th ed. (Worth Publishers, New York, 2013).
5. Kovas, Y., Haworth, C. M. A., Dale, P. S. & Plomin, R. The genetic and environmental origins of learning abilities and disabilities in the early school years. *Monogr. Soc. es. Child Dev.* **72,** vii–160 (2007).
6. Shakeshaft, N. G. *et al.* Strong genetic influence on a UK nationwide test of educational achievement at the end of compulsory education at age 16. *PLoS One* **8,** e80341 (2013).
7. Bartels, M., Rietveld, M. J. H., Van Baal, G. C. M. & Boomsma, D. I. Heritability of educational achievement in 12-year-olds and the overlap with cognitive ability. *Twin es.* **5,** 544–53 (2002).
8. Petrill, S. A. *et al.* Genetic and environmental influences on the growth of early reading skills. *J. Child Psychol. Psychiatry Allied Discip*. **51,** 660–667 (2010).
9. Wainwright, M. A., Wright, M. J., Luciano, M., Geffen, G. M. & Martin, N. G. Multivariate genetic analysis of academic skills of the Queensland core skills test and IQ highlight the importance of genetic g. *Twin es. Hum. Genet*. **8,** 602–608 (2005).
10. Kovas, Y. *et al.* Literacy and numeracy are more heritable than intelligence in primary school. *Psychol. Sci.* **24,** 2048–56 (2013).
11. Krapohl, E. *et al.* The high heritability of educational achievement reflects many genetically influenced traits, not just intelligence. *Proc. Natl. Acad. Sci. USA* **111,** 15273–15278 (2014).
12. Rimfeld, K., Kovas, Y., Dale, P. S. & Plomin, R. Pleiotropy across academic subjects at the end of compulsory education. *Sci. ep*. **5,** 11713 (2015).
13. Luo, Y. L. L., Kovas, Y., Haworth, C. M. A. & Plomin, R. The etiology of mathematical self-evaluation and mathematics achievement: Understanding the relationship using a cross-lagged twin study from ages 9 to 12. *Learn. Individ. Di er.* **21,** 710–718 (2011).
14. Kovas, Y. *et al.* Why children differ in motivation to learn: Insights from over 13,000 twins from 6 countries. *Pers. Individ. Dif.* **80,** 51–63 (2015).
15. Plomin, R. Genotype-environment correlation in the era of DNA. *Behav. Genet*. **44,** 629–38 (2014).
16. Haworth, C. M. A., Davis, O. S. P. & Plomin, R. Twins Early Development Study (TEDS): A genetically sensitive investigation of cognitive and behavioral development from childhood to young adulthood. *Twin es. Hum. Genet.* **16,** 117–25 (2013).
17. Rietveld, C. A. *et al.* GWAS of 126,559 individuals identifies genetic variants associated with educational attainment. *Science* **340,** 1467–71 (2013).
18. Davies, G. *et al.* Genetic contributions to variation in general cognitive function : a meta-analysis of genome-wide association studies in the CHARGE consortium (N 53 949). *Mol. Psychiatry* 1–10, doi: 10.1038/mp.2014.188 (2015).
19. Wray, N. R., Lee, S. H., Mehta, D., Vinkhuyzen, A. A. E. & Middeldorp, C. M. Research Review : Polygenic methods and their application to psychiatric traits. *J. Child Psychol. Psychiatry* **55,** 1068–1087 (2014).
20. Okbay, A. *et al.* Genome-wide association study identifies 74 loci associated with educational attainment. *Nature* (in press).
21. Krapohl, E. *et al.* Phenome-wide analysis of genome-wide polygenic scores. *Mol. Psychiatry* 1–6 (2015).
22. Asbury, K. & Plomin, R. *G is for Genes: e Impact of Genetics on Education and Achievement*. (John Wiley & Sons, 2013).
23. Haworth, C. M. A., Davis, O. S. P. & Plomin, R. Twins Early Development Study (TEDS): A Genetically Sensitive Investigation of Cognitive and Behavioral Development From Childhood to Young Adulthood. *Twin es. Hum. Genet.* 1–9, doi: 10.1017/thg.2012.91 (2013).
24. Price, T. S. *et al.* Infant zygosity can be assigned by parental report questionnaire data. *Twin es.* **3,** 129–133 (2000).
25. Rijsdijk, F. V. & Sham, P. C. Analytic approaches to twin data using structural equation models. *Brief. Bioinform*. **3,** 119–133 (2002).
26. McGue, M. & Bouchard, T. J. Adjustment of twin data for the effects of age and sex. *Behav. Genet*. **14,** 325–343 (1984).
27. Van Der Waerden B. L. On the sources of my book Moderne Algebra. *Hist. Math.* **2,** 31–40 (1975).
28. Lehmann, E. *Nonparametric Statistical Methods Based on an s*. (Holden-Day, San Francisco, CA, 1975).
29. Boker, S. *et al.* OpenMx: an open source extended structural equation modeling framework. *Psychometri a* **76,** 306–317 (2011).
30. Visscher, P. M. Power of the classical twin design revisited. *Twin es.* **7,** 505–512 (2004).
31. Visscher, P. M., Gordon, S. & Neale, M. C. Power of the classical twin design revisited: II detection of common environmental variance. *Twin es. Hum. Genet*. **11,** 48–54 (2008).
32. Medland, S. E. Alternate parameterization for scalar and non-scalar sex-limitation models in Mx. *Twin es.* **7,** 299–305 (2004).

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Author Contributions

Conceived and designed the experiments: K.R., Z.A. and R.P. Analyzed the data: K.R. and Z.A. Wrote the paper: K.R., Z.A., P.S.D., Y.K. and R.P. All authors reviewed the manuscript.

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Chapter 7: General discussion, implications and future directions

The aim of the thesis was to increase understanding of the aetiology of individual differences in educational attainment during compulsory education and beyond. The thesis mainly focused on educational achievement between ages 16 and 18 in the UK. Additionally, the EGCUT sample from made it possible to investigate whether heritability of educational attainment changes following a major change in the environment. The implications of each specific study are discussed in the chapters concerned and will not be repeated here. This chapter summarizes the key findings of the individual studies, and then draws together the overarching implications, discusses the limitations and proposes future research directions.

Summary of findings

Previous research has shown that educational achievement is highly heritable with around two-thirds of individual differences explained by inherited differences in children's DNA sequence. The high heritability of educational achievement in Western countries could be so substantial because of the relatively equal environmental opportunities provided for learning. For example, it has been suggested that the heritability of early reading ability (and pre-reading skills) is higher in Australia compared to Scandinavia because formal schooling at that age in Australia (but not in Scandinavia) equalises educational opportunity (Samuelsson et al., 2005). It is possible that the heritability of educational achievement in the UK is even greater for the same reason — at that age the UK educational curriculum is highly standardised, therefore, the environmental differences for schooling are reduced.

In Chapter 2, it was shown that the heritability of educational attainment changes substantially following a major environmental change using data from the Estonian Genome Centre, University of Tartu (EGCUT). Participants in the EGCUT cohort have studied and worked in Estonia when it was part of the Soviet Union and following a major shift in the environment – regaining the independence in Estonia. That allowed studying how the heritability of educational attainment and occupational status change in the same county following this major social change. Using a multi-method approach the results showed that in a more egalitarian society genetic differences between individuals explain twice the variance in these social outcomes compared to the Soviet era, which was less egalitarian. The finding that genetic influences on educational outcomes explain more variance when more equal opportunities are provided turns the current understanding of meritocracy on its head. The high heritability of educational and occupational outcomes can be viewed as an index of environmental opportunities in a society. That is, when the environmentally driven privilege is reduced then a larger proportion of individual differences is explained by genetic differences between them.

The work presented in this thesis then focused on the aetiology of school achievement and the aetiology of the causes and correlates of scholastic achievement in the UK. While much work has been conducted in understanding why children differ in English, science and mathematics, much less work has been conducted to understand why children differ in second language achievement. Chapter 3 showed that second language achievement is highly heritable (56%) much like achievement in other subjects, with a smaller proportion of individual differences explained by shared environmental (20%) and non-shared environmental factors (24%). In the most novel part of the study we showed that a third of the high heritability of second language achievement is explained by first language achievement, a third is explained by intelligence independent of first language achievement, and a further third is the unique genetic influence, independent of first language achievement or intelligence. This finding suggests that while there is strong evidence for pleiotropy in academic achievement, second language learning has substantial specific genetic influence that is not shared with general cognitive ability or achievement in the native language.

It is important to understand why individuals differ and to understand the causes and correlates of academic achievement, not least in order to facilitate the development of evidence-based educational policy and to help all children achieve their maximum potential. In Chapter 4 we showed that the high heritability of educational achievement is explained by a package of genetically influenced cognitive and non-cognitive traits. The results indicated that half of the high heritability of educational achievement is explained by intelligence, but all other cognitive and non-cognitive predictors, such as personality, self-efficacy, home and school environment, also explained a substantial and significant proportion of the heritability of school achievement; 50% of the heritability of educational achievement was explained by intelligence, while all cognitive and non-cognitive factors explained 75% of the heritability of GCSE grades all together. Phenotypically, these cognitive and non-cognitive factors explained 45% of the variance in exam grades.

While Chapter 4 assessed the general landscape of the heritability of school achievement, Chapter 5 focused on personality as a predictor of achievement at school. We showed that whereas personality is an important predictor of exam performance, explaining up to 6% of the variance in school grades, Grit (perseverance and passion for long term goals) adds little to the prediction, explaining only 0.5% of variance in school grades when other personality factors are controlled. We also showed that Grit is very similar to Conscientiousness both phenotypically (correlation of 0.53) and genetically (genetic correlation of 0.86). These findings question the current educational policies in the US and in the UK that target improving grit in students in order to improve their school performance.

Chapter 6 provided evidence that genetic factors influence both the appetite as well as aptitude for learning. At the end of compulsory education in the UK children can choose whether they want to continue their studies at A-level (General Certificate of Advanced Education), and around 50% of the students decide to do so, as a prerequisite for university education. Importantly, for the first time in their educational career they can freely choose what subjects they will continue to study. We showed that the heritability of the decision to continue their studies at A-level was 44%, but the heritability was even higher for the specific subjects they chose (52-80%). Importantly, the results also showed that despite the restriction of range, genetic differences continue to explain the individual differences in A-level exam performance.

Limitations

The general limitations of the twin design and DNA-based methods apply here, as discussed in Chapter 1. The more specific limitations that apply to specific analyses conducted are discussed in the chapters concerned.

Two other issues that should be noted concern the representativeness of twin samples (and volunteer-based population samples) and the issue of self-report and web-based data collection. Twins are an unusual subgroup, and it has been suggested that the analyses conducted on a twin sample might not be representative and might not generalise to singletons. Twins are more likely to suffer obstetric complications, and they have on average a shorter gestation time and lower birth weight. In addition, they are more likely to have developmental delays, especially in language development. Twins might be treated more similarly compared to singletons, especially MZ twins. However, the differences appear to be minor and even out over development (Hopper, Bishop, & Easton, 2005; Kendler, Martin, Heath, & Eaves, 1995; Knopik, Neiderhiser, DeFries, & Plomin, 2017).

Population-based volunteer samples might also not be entirely representative, as there could be a systematic bias between the individuals who accept the invitation to choose to participate compared to those who do not. For example, the UK Biobank sample invited around 9.2 million individuals to join the study, but the response rate was only 5.4%, which lead to ‘healthy volunteer’ selection bias (Fry et al., 2017). Because these systematic differences could bias the study results, it is important to ensure that a representative sample is achieved, including underrepresented population segments (Drivsholm et al., 2006; Kendler et al., 1995; Ridgeway et al., 2013). The EGCUT sample has been shown to be representative of the population in terms of age and sex (Leitsalu et al., 2015) and we showed that it is also representative in terms of educational attainment (Chapter 2); the TEDS sample has also been shown to be representative of the UK population of families with children (Chapters 3-5). However, it is not possible to completely rule out such a systematic error produced by the willingness to participate.

Self-report is also a limitation of this thesis, as the majority of the data collected relied on self-report. Self-report may be subject to social desirability bias, which can produce spurious relationships, or in multivariate studies can act as a suppressor to hide the true relationship between variables (Podsakoff, MacKenzie, Lee, & Podsakoff, 2003). In the present thesis we checked the self-reported exam results at the end of compulsory education to the exam grades recorded in the National Pupil Database (NPD) and they yielded a correlation of 0.99 on average indicating that self-reported educational achievement measures were not subject to this bias.

Additionally, most data collected in TEDS involved web-based batteries, rather than in-person assessments. Genetic analyses, such as those used in the present thesis, need large samples to have adequate power, making it difficult to collect data in person. However, it has been argued that while online testing leads to increased sample size, this comes at a cost of representativeness (Germine et al., 2012). Extra effort must be made to maintain the representativeness of the sample. Furthermore, online testing could lead to decreased data quality, because data collection is done remotely, without experimenter supervision and instructions (Germine et al., 2012). Nevertheless, there is some evidence that participants actually pay more attention to instructions when data collection is done remotely (Ramsey, Thompson, McKenzie, & Rosenbaum, 2016). Moreover, there is now evidence that there are no significant or systematic differences in the results when comparing data collected online to those collected remotely (over web) for either questionnaire measures (Casler, Bickel, & Hackett, 2013) or cognitive measures (Germine et al., 2012; Haworth et al., 2007).

Implications and future directions

Implications of each individual study presented in this thesis are discussed within each specific chapter. This section discusses the overarching implications of the thesis. It considers the aetiology of educational achievement and the value of understanding the genetic influence on educational outcomes. Specifically it discusses the possible avenues of an educational curriculum adopting a more individualised approach to learning. Proposals for future work will also be discussed.

The aetiology of educational achievement

There is converging evidence for genetic influence on virtually every complex trait (Polderman et al., 2015), and this also holds for educational achievement. Over two-thirds of differences in educational achievement, from early school years to the end of compulsory education, and even at A-level are explained by inherited differences in children's DNA sequence, rather than environmental factors. This high heritability is observed for both achievement in humanities and STEM (Science, Technology Engineering and Mathematics) subjects, as well as for more 'creative' subjects such as art and music.

A reasonable assumption is that the substantial genetic influence observed in this thesis is explained by general cognitive ability (intelligence). Intelligence is one of the strongest predictors of school achievement (Calvin et al., 2012; Deary, Strand, Smith, & Fernandes, 2007), and behavioural genetic studies have shown that intelligence is also substantially heritable, with around half of the variance in intelligence explained by the inherited differences in the DNA sequence (Deary, 2012; Krapohl et al., 2014; Plomin & Deary, 2015). Furthermore, the links between achievement and intelligence have been shown to be mediated by genetic factors (Bartels, Rietveld, Van Baal, & Boomsma, 2002; Calvin et al., 2012; Petrill & Wilkerson, 2000). Importantly, however, we showed here that while half of the genetic variance in exam results is explained by intelligence, many other traits also contribute to this high heritability, such as personality, self-efficacy, perceptions of home and school environment.

This suggests that the high heritability of educational achievement at this crucial part of children's educational career, measured by the exams at the end of compulsory education, is effectively a composite measure and reflects many cognitive and non-cognitive traits (Chapter 4).

An interesting facet of this research is that heritability estimates can change quite drastically with major changes in the environment. SNP heritability and GPS heritability were twice as high during the post-Soviet era in Estonia compared to the Soviet era. One of the possible interpretation of this finding is that in a more equalitarian society genetic differences between children account for more variance compared to a less equal society. If environmental differences between individuals are attenuated, then genetic differences account for most of the individual differences (Chapter 2). These results indicate that high heritability of educational outcomes could be considered as an index of more equal opportunity in a society. The findings also imply that the studies conducted in Western societies more recently might not generalise to other populations and other age groups. While we have always known that heritability is a population statistic that tells us the proportion of individual differences that are explained by genetic factors in a particular population at a particular time, what is and not what could be (Knopik et al., 2017), we have provided empirical evidence of how much these estimates can change with a massive social change. Additionally, most molecular genetic research to date has been conducted on individuals with European descent, not considering Asian or African ancestry. It is possible that the common genetic variance that contributes to the variation of complex traits is shared across theses ethnicities, but equally there could be variation within ethnicities and the some educationally relevant loci could be different in frequency and effect size across different ethnicity groups (Visscher et al., 2017). This suggests that more research is needed to understand the aetiology of educational achievement and understand the predictors and correlates in other countries using different age groups considering the diverse educational systems around the world.

Genetics does not only influence aptitude (school grades) but also appetite (choice; A-levels) for learning (Chapter 5). Interestingly, the choice about continuing studies is in equal proportions explained by shared environmental and non-shared environmental factors, which makes it one of the largest shared environmental influences found for any complex trait. The specific subject choices on the other hand are even more influenced by genetic factors. This might imply that educational achievement is increasingly influenced by complex gene-environment correlation. To the extent that children are given more choice about their education then these decisions could be based on their genetic predispositions. This complex gene-environment correlation could partly explain the high heritability of educational achievement at the end of compulsory education as children are increasingly selecting, modifying and evoking environmental experiences partly based on their genetic propensities.

The DNA revolution

The past decade has seen many scientific discoveries made through genome-wide association (GWA) studies, which aim to identify the genetic loci (e.g., single nucleotide polymorphisms, SNPs) associated with a trait of interest. The GWA studies have provided evidence for substantial pleiotropy--the same genetic variants influence multiple traits - but also provided evidence for substantial polygenicity, whereby all complex traits are influenced by very many genetic variants all of small effect. This indicates that each individual carries many alleles that contribute positively to complex traits and many alleles that contribute negatively to traits, meaning that it is possible that each individual has a unique combination of trait associated set of alleles (Visscher et al., 2017). We have also learned that the SNPs associated with a trait of interest are correlated with the GWA sample size, so with increasing sample size the number of associated variants discovered increases (Visscher, Brown, McCarthy, & Yang, 2012). This has encouraged collaboration of scientists around the world, with an increasing number of consortia established, and this collaboration has been very successful for molecular genetic research in particular. One of the most notable GWA studies that is linked to the topic of this thesis is adult years of education (*EduYears*), a GWA study that included over 297,000 participants and identified 74 genome-wide significant variants associated with educational attainment (Okbay et al., 2016).

It is now possible to calculate genome-wide polygenic scores (GPS) that capitalise on the summary statistics of GWA studies (see Chapter 2 for details). This method offers an individualised prediction of academic achievement from DNA alone. This method is especially powerful as it uses the summary statistics of independent GWA sample, therefore the prediction from GPS to trait must be entirely due to genetics as it is not confounded by the environmental factors (Visscher et al., 2017). Research has shown that the adult *EduYears* GPS predicts up to 9% of variance in educational achievement at the end of compulsory education, although the prediction at earlier school years is smaller (Selzam, Krapohl, et al., 2017). It is notable, however, that educational achievement is highly heritable across school years, so this finding is surprising. It is possible that the closer the target sample is in age to the GWA sample the more variance in educational achievement is explained; for example if GWA study was conducted on academic achievement at the age of 7, then we predict that a GPS derived from summary statistics of that GWA would predict more variance in achievement in compulsory education, and less variance in the years of schooling phenotype. Another reason why *EduYears* GPS predicts best at the end of compulsory education is the fact that GCSE grades are strongly associated with whether or not individuals pursue university studies. The increased prediction of educational achievement from *EduYears* GPS over development could also be explained in terms of gene-environment correlation. Gene-environment correlation is increasingly important as children progress from primary school to secondary school culminating with GCSE exams, because children increasingly select, modify and evoke their educational experiences partly based on their genetic propensities. Notably, genetic factors not only affect educational achievement per se, but they also affect the environments children choose, thus influencing both the aptitude and appetite for learning (Knopik et al., 2017; Rimfeld, Ayorech, Dale, Kovas, & Plomin, 2016; Shakeshaft et al., 2013).

However, it is not clear whether the stronger prediction at age of 16 is due to the reliability of the achievement measures, whether the prediction is stronger for the overall academic achievement composite or for specific subjects learned at school, or whether the increased prediction at age 16 is due to exam taking skill. Furthermore, it is not clear whether this prediction from adult *EduYears* GPS to academic achievement during childhood is simply explained by the variance in intelligence that is captured by adult educational attainment GWA. These are issues that I hope to address in my future research.

EduYears GPS has been shown to be associated with reading ability, cognitive ability, family SES, and to a smaller extent with behavioural problems (Krapohl et al., 2015; Selzam, Dale, et al., 2017; Selzam, Krapohl, et al., 2017), providing further evidence for substantial pleiotropy in educationally relevant traits. This is in line with the results provided in the present thesis, indicating that educational achievement reflects many genetically influenced cognitive and non-cognitive traits. Understanding the genetics of educational achievement, and the precursors, such as cognitive ability, reading ability, personality, could help to understand the biological pathways of learning and may therefore aid in providing individualised interventions (Cesarini & Visscher, 2017).

The major advantage of GPS is that it enables prediction of educational outcomes from birth or even prenatally. No other phenotype, except family SES, which is itself genetically influenced, is able to provide such good prediction from very early on. Importantly, GPS offers additional prediction to family SES as children from the same family (same SES) could have very different educational outcomes, and siblings only share 50% of their segregating genes on average. Studying genotyped DZ twins would allow us to estimate this additional layer of within-family prediction added to the family-wide measures, such as SES. Knowing individual-specific genetic predispositions from birth would allow educationalists to develop early interventions and personalised education plans for children who might be genetically predisposed for having learning difficulties. And, on the other hand, it is possible to identify children with exceptional talent and offer them personalised learning programs so that they can reach their maximum potential. With personalised education it is possible to target the whole distribution of learning abilities, interests and preferences. This GPS prediction is not currently powerful enough to provide specific individualised prediction, but it is sufficiently powerful to explain group differences in a population. For example, it is possible to group individuals with the highest educationally relevant GPS and individuals with the lowest GPS, individuals with the highest genetic risk of developing learning difficulties (Cesarini & Visscher, 2017; Dudbridge, 2013; Visscher et al., 2017). These GPS will be increasingly predictive with more powerful discovery GWA studies. It has been estimated that with around 2 million individuals in GWA sample GPS will provide the predictive power of the current SNP heritability (~20%) (Cesarini & Visscher, 2017).

We know that the heritability of educational achievement is around 60% (Bartels et al., 2002; Coventry et al., 2012; Kovas, Haworth, Dale, & Plomin, 2007; Krapohl et al., 2014; Petrill et al., 2010; Rimfeld et al., 2016; Rimfeld, Kovas, Dale, & Plomin, 2015; Shakeshaft et al., 2013; Wadsworth, DeFries, Fulker, & Plomin, 1995; Wainwright, Wright, Geffen, Luciano, & Martin, 2005), and that SNP heritability is also substantial (Krapohl & Plomin, 2016; Rimfeld et al., 2015), so predicting 9% of variance might seem meagre. However, we probably are only at the beginning of harnessing the power of GWA. The power and prediction of GPS will increase with more powerful GWA discovery studies. Another more powerful GWA of educational attainment is currently underway involving over 1.3 million participants, which is likely to be a game changer in terms of offering better power for a GPS that can more accurately predict educational outcomes from very early on.

Meaning of heritability

It is important to reiterate what heritability means and does not mean. In terms of quantitative genetic research (both using family design and DNA based methods) that estimates the relative contribution of genetic factors to the variance or covariance in the trait of interest, heritability does not imply immutability; it predicts *what is*, not what *could be* or *should be*. Although a substantial proportion of individual differences is attributable to genetic factors, a substantial proportion of individual differences is attributable to environmental influences as well (Knopik et al., 2017).

The aetiology of educational achievement can change with changes in environment, as shown in the present thesis. Our findings suggest that if environmental variance is reduced then a larger proportion of individual differences remaining would be accounted for by genetic differences between individuals. Therefore, finding substantial genetic influence on a complex trait tells us nothing about the potential of environmental interventions. One example for this is weight, which is around 70% heritable (Maes, Neale, & Eaves, 1997; Stunkard, 1986), yet with major environmental intervention, such as diet and exercise program, almost everybody would lose weight, although it would be easier for some than others.

A classic example is a rare inherited disease phenylketonuria (PKU) that interferes with how the body breaks down protein in foods into amino acids. Leaving the disease untreated can lead to severe brain damage and intellectual disability, yet with a simple environmental intervention -- a special diet -- this brain damage is preventable (Diamond, Prevor, Callender, & Druin, 1997; Knopik et al., 2017). Therefore, the substantial genetic influence on a trait such as educational achievement does not restrict the potential of environmental interventions (Cesarini & Visscher, 2017; Knopik et al., 2017). Genes do not necessarily influence outcomes through purely physiological ways, because genetic factors influence many traits related to learning, such as motivation, personality, behavioural problems or concentration (Cesarini & Visscher, 2017).

However, continuing with the weight example, losing weight is easier for some individuals and harder for others, therefore, personalised treatment is recommended in order to achieve successful outcomes. If we translate this to education, then we know that with similar educational environments some children will find learning harder than the others. Hence, personalising educational experiences that are correlated with children's genetic propensities is likely to improve results. It would be of considerable interest to empirically study how genetics could help educationalists to personalise learning programs. We are already seeing the first studies of therapygenetics for anxiety disorders using DNA markers (polygenic scores) to test the differential susceptibility hypothesis, showing that genetic predisposition could moderate intervention effects (Keers et al., 2016). This line of research, if successful, could facilitate personalised intervention for education too, as it could inform educationalists which intervention is most likely to be most successful for each individual.

While the advances in molecular genetic studies have been remarkable, we still do not understand the biological mechanisms underlying educational achievement and the correlates of school performance. Nonetheless, quantitative genetic studies, as presented in the present thesis, advance the understanding of causes and correlates of educational achievement. The most exciting direction for research is to identify the inherited DNA variants responsible for the high heritability of educationally relevant traits. The GPS leads the way in this new and exciting research, with the predictive accuracy increasing with more powerful discovery studies. It has been predicted that the predictive power of educationally relevant GPS reaches the SNP heritability soon. However, there is much discrepancy about the SNP heritability (ranges between 15-30%) for educational achievement, because it can change when environmental opportunities change, as shown in the present thesis, but can also change because of phenotypic and/or genetic heterogeneity across cohorts (Visscher et al., 2017). Finding genes and understanding the biological pathways will have far-reaching implications for research bringing together different disciplines of research in order to increase the understanding of learning, thus facilitating interdisciplinary research. It will also affect society more generally, where we might hope that greater knowledge will improve the decision-making. It is important to start discussions with policy makers to consider societal and ethical implications of genetic research, so that this increased understanding of genetic influence on educational achievement, especially prediction from DNA, will benefit children and society as a whole (Knopik et al., 2017).

Personalised education

Educational policy has been reluctant to consider genetic influence on educational outcomes. The standardised curriculum implemented at schools assumes that children are similar and that the same curricula are suitable for all. Finding that individual differences in school achievement are to a large extent explained by inherited differences in children's DNA sequence challenges this view. Rather than providing 'one-size-fits-all' curricula, a more individualised approach is needed that recognises that children are different, and that these differences are substantially explained by genetic factors, as well as by the interplay between genes and environment.

When children are taught the same way regardless of their abilities then some children in the classroom are overly challenged and others are bored, and only some children learn at their right level. Children differ in how and how much they learn largely because of the genetic differences between them; educational policies could benefit from accepting this knowledge (Asbury & Plomin, 2013; Haworth, Asbury, Dale, & Plomin, 2011; Shakeshaft et al., 2013). Genetically sensitive approaches to learning recognise that children actively choose educational environments that are correlated with their genetic propensities. As shown in the present thesis genetics affects both the aptitude and appetite for learning. This gene-environment correlation means that children add value to their own educational experiences; they are naturally drawn to people and experiences that they find easier or more engaging (Asbury & Plomin, 2013; Haworth et al., 2011). More individualised learning programs would not only try to feed the information to children, but would nurture their individual talents and abilities.

GPS prediction could help with personalised education, for example, when we can move from educationally relevant alleles to identifying loci (and then calculating GPS) associated with more specific phenotypes, such dyslexia or dyscalculia, we could identify children who are at risk and enrol them to early intervention programs to ensure they reach basic reading and mathematical skills, and in some cases we might be able to help children before they express the phenotype. Several neurodevelopmental disorders have been shown to be associated with learning disabilities or difficulties at school, for example autism, ADHD, epilepsy - all of which are substantially heritable.

Understanding the genetic aetiology of these disorders and their covariation with learning difficulties is very valuable, because it will facilitate genomic prediction that could help with aetiological diagnoses and ultimately with prevention and intervention. It might be possible to diagnose specific learning disabilities using genomic data rather than only symptoms, and offer children personalised learning programs tailored to their genetic propensities.

I think that children would benefit from more choice in the classroom, and teachers would benefit from more freedom to adjust the learning activities for children's needs. Teachers realise that children are not blank slates that can be moulded to yield the same outcomes. Given more freedom in the curriculum teachers would naturally cater for the different learning styles and needs of every student. They would draw out the talents of individual children in the classroom, and they could plan the learning accordingly. Policy makers would benefit from understanding that children are different in part because of genetic differences between them, and therefore that it may not be wise to measure teacher quality just from pupils' achievement at each year as they progress through the National curriculum – but rather teacher effectiveness could reflect supporting progress and potential (Asbury & Plomin, 2013). All schooling programs are already personalised to a certain extent, for example children with specific learning difficulties and taught by a specific teacher; genetic prediction using GPS could be a useful addition to the individualised approaches already in place (Asbury & Plomin, 2013; Cesarini & Visscher, 2017).

While I argue for the support of personalised education, this does not mean that children should not be taught the basic skills. Children should be taught basic reading and mathematics skills as well as basic computer skills needed to comfortably live in the rapidly developing technological society as these form the building blocks for almost all areas of learning. However, teaching these basic skills can also be personalised. Classrooms would benefit from technology that tracks children's progress and caters for their skills and knowledge; for example in mathematics, such software is already in use that tracks the mistakes children make and offer more examples for individual pupils whenever a topic is not clear. The trend towards personalised learning will become more practical with rapid developments in technology and educational software that is tailored to the individual aptitudes, appetites and needs of children.

There is also a need for more longitudinal research to understand the causes of individual differences and to identify children who might best benefit from specific interventions. Identifying early environmental risk factors could allow for the development of environmental risk score that could be used together with genomic prediction. This multi-prediction approach may provide a powerful tool for the educationalist to provide a child specific learning programs and to tailor more effective interventions.

Future work

If molecular genetic research were able to identify all genetic variants involved in educational achievement, then there would be no need to estimate genetic influence on traits using quantitative genetic methods such as twin studies, as it would be possible to do it using the specific DNA variants only. But this seems unlikely in the foreseeable future, because of the substantial polygenicity described above (Knopik et al., 2017). On the other hand, while molecular genetic approaches are mainly about genetic influences, quantitative genetic research is about genetic and environmental influences. Quantitative genetic methods estimate the cumulative effect of genetic and environmental influences on the variance of a trait influences involved. It is therefore, for example, possible to use quantitative genetic methods to control for genetic effects on trait when studying environmental influences on a trait, and vice versa (Knopik et al., 2017). This line of research is part of my future research programme.

There is now converging evidence for the heritability of educational achievement across school years (Kovas et al., 2007; Rimfeld et al., 2016; Shakeshaft et al., 2013). However, existing evidence does not indicate whether the genetic factors contributing to individual differences in educational achievement at different stages in the curriculum are the same, or whether different genes contribute to the heritability of achievement at different stages in development. Previous research has shown that genetic and shared environmental factors display substantial stability while non-shared environmental factors contribute to change in English, mathematics and science over the primary school years (Kovas et al., 2007). However, surprisingly little is known about the stability and change of educational achievement across the school years, from primary to secondary education and beyond. Longitudinal analyses of reading ability have shown that stability of word recognition from childhood to adolescence is largely explained by genetic factors (age to age genetic correlations of 1.0) (Wadsworth, Corley, Hewitt, & Defries, 2001). Conversely, the longitudinal analyses of reading comprehension showed that stability is partly explained by genetic factors (57%) and shared-environmental factors also contributed to the stability of reading (36%) in the middle childhood (Malanchini et al., 2017). However, school achievement involves much more than reading; to my knowledge, no longitudinal analysis has been conducted studying continuity and change of educational achievement throughout compulsory education, which is part of my future research plans. Furthermore, it is not clear whether genetic stability is explained by general cognitive ability, which has also been shown to be substantially heritable (Deary et al., 2012; Deary, Spinath, & Bates, 2006), or what other cognitive or non-cognitive traits explain the stability or change in school achievement; this is also part of my future research program.

We know very little about the mechanisms by which genetic factors influence individual differences in school achievement, and we know even less about how these common genetic variants influence continuity of scholastic achievement from age to age. The full understanding of biological mechanisms will become clearer once the specific genetic variants influencing school performance are identified. However, we are unlikely to fully understand the biological pathways of genetic variants influencing scholastic achievement since the effect sizes of individual genetic variants are very small (Knopik et al., 2017; Kovas et al., 2007).

In the shorter term, it is useful to extend the polygenic score prediction research, which has already been shown to explain a meaningful portion of variance in overall academic achievement (Selzam, Krapohl, et al., 2017). For example, it would be useful to examine the individual academic subjects children study at school, and to investigate why a larger proportion of variance is explained in overall achievement at 16 as compared to earlier ages. A possible explanation is the relative reliability of achievement measures across age, which could vary between teacher ratings and exam scores. Another possibility is that the stronger prediction at the end of compulsory education may be due to exam-taking or increased gene-environment correlation over development. Furthermore, it is not clear whether this prediction from adult *EduYears* GPS to academic achievement during childhood is simply explained by intelligence captured by the adult educational attainment GWA. I hope to explore all of this further, especially with the more powerful GWA studies that will soon be available.

Another possible research direction is to use polygenic scores in gene-environment interplay research. The gene-environment interaction literature to date, for example, has a high rate of false-positive results, where findings do not replicate. This might be due to the small effect of associated alleles used in the genotype-environment interaction research. Using GPS would hopefully mitigate this problem as GPS have much greater predictive power than single SNPs or single genes (Okbay et al., 2016). Studying the heterogeneity in educational attainment in different populations and birth cohorts, in urban and rural areas, and in different cultures is largely unexplored. GPS offer a good research tool to explore this research avenue further. Using GPS enables powerful studies to examine whether certain environments amplify or dampen the genetic influence on complex traits such as educational achievement. GPS analyses will likely facilitate research into the links between genome and epigenome, transcriptome, microbiome, and then eventually behaviour. For example, a promising new area is to study responses to drug treatments, and similar approach could be taken to help children with developmental disorders or learning difficulties. Eventually interdisciplinary research that integrates different disciplines provides the best hope for personalised intervention and learning programs.

Conclusion

To conclude, the present thesis addressed several questions related to the aetiology and correlates of educational achievement, which had been previously unexplored. The findings of this thesis support the trend towards personalised education that accounts for individual differences rather than providing a one-size-fits-all curriculum. Although the findings of this thesis contribute to the overall understanding of the complex aetiology of educational achievement and the associated cognitive and non-cognitive traits, many questions remain unanswered, as discussed in this concluding chapter. Longitudinal modelling and molecular genetic approaches in particular offer promise to advance the understanding of educational achievement, and addressing these outstanding questions is part of my future research plans.

References

Asbury, K., & Plomin, R. (2013). *G is for Genes: The Impact of Genetics on Education and Achievement*. John Wiley & Sons.

Bartels, M., Rietveld, M. J. H., Van Baal, G. C. M., & Boomsma, D. I. (2002). Heritability of educational achievement in 12-year-olds and the overlap with cognitive ability. *Twin Research : The Official Journal of the International Society for Twin Studies*, *5*(6), 544–53. http://doi.org/10.1375/136905202762342017

Calvin, C. M., Deary, I. J., Webbink, D., Smith, P., Fernandes, C., Lee, S. H., … Visscher, P. M. (2012). Multivariate genetic analyses of cognition and academic achievement from two population samples of 174,000 and 166,000 school children. *Behavior Genetics*, *42*(5), 699–710. http://doi.org/10.1007/s10519-012-9549-7

Casler, K., Bickel, L., & Hackett, E. (2013). Separate but equal? A comparison of participants and data gathered via Amazon's MTurk, social media, and face-to-face behavioral testing. *Computers in Human Behavior*, *29*(6), 2156–2160. http://doi.org/10.1016/j.chb.2013.05.009

Cesarini, D., & Visscher, P. M. (2017). Genetics and educational attainment. *Npj Science of Learning*, *2*(1), 4. http://doi.org/10.1038/s41539-017-0005-6

Coventry, W., Antón-Méndez, I., Ellis, E. M., Levisen, C., Byrne, B., van Daal, V. H. P., & Ellis, N. C. (2012). The etiology of individual differences in second language acquisition in Australian school students: A behavior-genetic study. *Language Learning*, *62*, 880–901. http://doi.org/10.1111/j.1467-9922.2012.00718.x

Deary, I. J. (2012). Intelligence. *Annual Review of Psychology*. http://doi.org/10.1146/annurev-psych-120710-100353

Deary, I. J., Spinath, F. M., & Bates, T. C. (2006). Genetics of intelligence. *European Journal of Human Genetics : EJHG*, *14*(6), 690–700. http://doi.org/10.1038/sj.ejhg.5201588

Deary, I. J., Strand, S., Smith, P., & Fernandes, C. (2007). Intelligence and educational achievement. *Intelligence*, *35*(1), 13–21. http://doi.org/10.1016/j.intell.2006.02.001

Deary, I. J., Yang, J., Davies, G., Harris, S. E., Tenesa, A., Liewald, D., … Visscher, P. M. (2012).

Genetic contributions to stability and change in intelligence from childhood to old age. *Nature*. http://doi.org/10.1038/nature10781

Diamond, A., Prevor, M. B., Callender, G., & Druin, D. P. (1997). Prefrontal cortex cognitive deficits in children treated early and continuously for PKU. *Monographs of the Society for Research in Child Development*, *62*(4), 1–208. http://doi.org/10.2307/1166208

Drivsholm, T., Eplov, L. F., Davidsen, M., Jørgensen, T., Ibsen, H., Hollnagel, H., & Borch-Johnsen, K. (2006). Representativeness in population-based studies: a detailed description of non-response in a Danish cohort study. *Scandinavian Journal of Public Health*, *34*(6), 623–631. http://doi.org/10.1080/14034940600607616

Dudbridge, F. (2013). Power and predictive accuracy of polygenic risk scores. *PLoS Genetics*, *9*(3), e1003348. http://doi.org/10.1371/journal.pgen.1003348

Fry, A., Littlejohns, T. J., Sudlow, C., Doherty, N., Adamska, L., Sprosen, T., … Allen, N. E. (2017). Comparison of sociodemographic and health-related characteristics of UK Biobank participants with the general population. *American Journal of Epidemiology*, advanced online publication.

Germine, L., Nakayama, K., Duchaine, B. C., Chabris, C. F., Chatterjee, G., & Wilmer, J. B. (2012). Is the Web as good as the lab? Comparable performance from Web and lab in cognitive/perceptual experiments. *Psychonomic Bulletin & Review*, *19*(5), 847–857. http://doi.org/10.3758/s13423-012-0296-9

Haworth, C. M. A., Asbury, K., Dale, P. S., & Plomin, R. (2011). Added value measures in education show genetic as well as environmental influence. *PloS One*, *6*(2), e16006. http://doi.org/10.1371/journal.pone.0016006

Haworth, C. M. A., Harlaar, N., Kovas, Y., Davis, O. S. P., Oliver, B. R., Hayiou-Thomas, M. E., … Plomin, R. (2007). Internet cognitive testing of large samples needed in genetic research. *Twin Research and Human Genetics : The Official Journal of the International Society for Twin Studies*, *10*(4), 554–63. http://doi.org/10.1375/twin.10.4.554

Hopper, J. L., Bishop, D. T., & Easton, D. F. (2005). Population-based family studies in genetic epidemiology. *Lancet*, *366*(9494), 1397–1406. http://doi.org/10.1016/S0140-6736(05)67570-8

Hugh-Jones, D., Verweij, K. J. H., St. Pourcain, B., & Abdellaoui, A. (2016). Assortative mating on educational attainment leads to genetic spousal resemblance for polygenic scores. *Intelligence*, *59*, 103–108. http://doi.org/10.1016/j.intell.2016.08.005

Keers, R., Coleman, J. R. I., Lester, K. J., Roberts, S., Breen, G., Thastum, M., … Eley, T. C. (2016). A genome-wide test of the differential susceptibility hypothesis reveals a genetic predictor of differential response to psychological treatments for child anxiety disorders. *Psychotherapy and Psychosomatics*, *85*(3), 146–158. http://doi.org/10.1159/000444023

Kendler, K. S., Martin, N. G., Heath, A. C., & Eaves, L. J. (1995). Self-report psychiatric symptoms in twins and their nontwin relatives: Are twins different? *American Journal of Medical Genetics - Neuropsychiatric Genetics*, *60*(6), 588–591. http://doi.org/10.1002/ajmg.1320600622

Knopik, V. S., Neiderhiser, J. M., DeFries, J. C., & Plomin, R. (2017). *Behavioral Genetics. 7th ed.*

Worth Publishers, New York.
Kong, A., Frigge, M. L., Thorleifsson, G., Stefansson, H., Young, A. I., Zink, F., … Stefansson, K. (2017). Selection against variants in the genome associated with educational attainment. *Proceedings of the National Academy of Sciences*, *114*(5), E727-32. http://doi.org/10.1073/pnas.1612113114
Kovas, Y., Haworth, C. M. A., Dale, P. S., & Plomin, R. (2007). The genetic and environmental origins of learning abilities and disabilities in the early school years. *Monographs of the Society for Research in Child Development*, *72*(3), 1–144. http://doi.org/10.1111/j.1540-5834.2007.00439.x
Krapohl, E., Euesden, J., Zabaneh, D., Pingault, J., Rimfeld, K., Stumm, S. Von, … Plomin, R. (2015). Phenome-wide analysis of genome-wide polygenic scores. *Molecular Psychiatry*, (21), 1188–1193. http://doi.org/10.1038/mp.2015.126
Krapohl, E., & Plomin, R. (2016). Genetic link between family socioeconomic status and children's educational achievement estimated from genome-wide SNPs. *Molecular Psychiatry*, *21*, 437–443. http://doi.org/10.1038/mp.2015.2
Krapohl, E., Rimfeld, K., Shakeshaft, N. G., Trzaskowski, M., McMillan, A., Pingault, J.-B., … Plomin, R. (2014). The high heritability of educational achievement reflects many genetically influenced traits, not just intelligence. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(42), 15273–15278. http://doi.org/10.1073/pnas.1408777111
Leitsalu, L., Haller, T., Esko, T., Tammesoo, M. L., Alavere, H., Snieder, H., … Metspalu, A. (2015). Cohort profile: Estonian Biobank of the Estonian Genome Center, University of Tartu. *International Journal of Epidemiology*, *44*(4), 1137–1147. http://doi.org/10.1093/ije/dyt268
Maes, H. H. M., Neale, M. C., & Eaves, L. J. (1997). Genetic and environmental factors in relative body weight and human adiposity. *Behavior Genetics*. http://doi.org/10.1023/A:1025635913927
Malanchini, M., Wang, Z., Voronin, I., Schenker, V. J., Plomin, R., Petrill, S. A., & Kovas, Y. (2017). Reading self-perceived ability, enjoyment and achievement: A genetically informative study of their reciprocal links over time. *Developmental Psychology*, *53*(4), 698–712. http://doi.org/10.1037/dev0000209
Okbay, A., Beauchamp, J. P., Fontana, M., Lee, J. J., Pers, T. ., Rietveld, C. A., … Pickrell, J. K. (2016). Genome-wide association study identifies 74 loci associated with educational attainment. *Nature*, *533*(7604), 539–542. http://doi.org/10.1038/nature17671
Petrill, S. A., Hart, S. A., Harlaar, N., Logan, J., Justice, L. M., Schatschneider, C., … Cutting, L. (2010). Genetic and environmental influences on the growth of early reading skills. *Journal of Child Psychology and Psychiatry and Allied Disciplines*, *51*, 660–667. http://doi.org/10.1111/j.1469-7610.2009.02204.x
Petrill, S. A., & Wilkerson, B. (2000). Intelligence and achievement: A behavioral genetic perspective. *Educational Psychology Review*, *12*(2), 185–199. http://doi.org/10.1023/A:1009023415516
Plomin, R., & Deary, I. J. (2015). Genetics and intelligence differences: five special findings.

Molecular Psychiatry, (20(1)), 98–108. http://doi.org/10.1038/mp.2014.105

Podsakoff, P. M., MacKenzie, S. B., Lee, J. Y., & Podsakoff, N. P. (2003). Common method biases in behavioral research: a critical review of the literature and recommended remedies. *Journal of Applied Psychology*, *88*(5), 879–903. http://doi.org/10.1037/0021-9010.88.5.879

Polderman, T. J. C., Benyamin, B., de Leeuw, C. A., Sullivan, P. F., van Bochoven, A., Visscher, P. M., & Posthuma, D. (2015). Meta-analysis of the heritability of human traits based on fifty years of twin studies. *Nature Genetics*, *47*(7), 702–709. http://doi.org/10.1038/ng.3285

Ramsey, S. R., Thompson, K. L., McKenzie, M., & Rosenbaum, A. (2016). Psychological research in the internet age: The quality of web-based data. *Computers in Human Behavior*, *58*, 354–360. http://doi.org/10.1016/j.chb.2015.12.049

Ridgeway, J. L., Han, L. C., Olson, J. E., Lackore, K. A., Koenig, B. A., Beebe, T. J., & Ziegenfuss, J. Y. (2013). Potential bias in the bank: What distinguishes refusers, nonresponders and participants in a clinic-based biobank? *Public Health Genomics*, *16*(3), 118–126. http://doi.org/10.1159/000349924

Rimfeld, K., Ayorech, Z., Dale, P. S., Kovas, Y., & Plomin, R. (2016). Genetics affects choice of academic subjects as well as achievement. *Scientific Reports*, *6*, 26373. http://doi.org/10.1038/srep26373

Rimfeld, K., Kovas, Y., Dale, P. S., & Plomin, R. (2015). Pleiotropy across academic subjects at the end of compulsory education. *Scientific Reports*, *5*, 11713. http://doi.org/10.1038/srep11713

Samuelsson, S., Byrne, B., Quain, P., Wadsworth, S., Corley, R., DeFries, J. C., … Olson, R. (2005). Environmental and genetic influences on prereading skills in Australia, Scandinavia, and the United States. *Journal of Educational Psychology*. http://doi.org/10.1037/0022-0663.97.4.705

Selzam, S., Dale, P. S., Wagner, R. K., DeFries, J. C., Cederlöf, M., O'Reilly, P. F., … Plomin, R. (2017). Genome-wide polygenic scores predict reading performance throughout the school years. *Scientific Studies of Reading*, 1–16. http://doi.org/10.1080/10888438.2017.1299152

Selzam, S., Krapohl, E., von Stumm, S., O'Reilly, P. F., Rimfeld, K., Kovas, Y., … Plomin, R. (2017). Predicting educational achievement from DNA. *Molecular Psychiatry*, *22*, 267–272. http://doi.org/10.1038/mp.2016.107

Shakeshaft, N. G., Trzaskowski, M., McMillan, A., Rimfeld, K., Krapohl, E., Haworth, C. M. A., … Plomin, R. (2013). Strong genetic influence on a UK nationwide test of educational achievement at the end of compulsory education at age 16. *PLoS ONE*, *8*, e80341. http://doi.org/10.1371/journal.pone.0080341

Stunkard, A. J. (1986). A twin study of human obesity. *JAMA: The Journal of the American Medical Association*, *256*(1), 51. http://doi.org/10.1001/jama.1986.03380010055024

Visscher, P. M., Brown, M. A., McCarthy, M. I., & Yang, J. (2012). Five years of GWAS discovery. *American Journal of Human Genetics*. http://doi.org/10.1016/j.ajhg.2011.11.029

Visscher, P. M., Wray, N. R., Zhang, Q., Sklar, P., McCarthy, M. I., Brown, M. A., & Yang, J. (2017). 10 Years of GWAS discovery: Biology, function, and translation. *The American Journal of*

Human Genetics, *101*(1), 5–22. http://doi.org/10.1016/j.ajhg.2017.06.005

Wadsworth, S. J., Corley, R. P., Hewitt, J. K., & Defries, J. C. (2001). Stability of genetic and environmental influences on reading performance at 7, 12, and 16 years of age in the Colorado Adoption Project. *Behavior Genetics*, *31*(4), 353–359. http://doi.org/10.1023/A:1012218301437

Wadsworth, S. J., DeFries, J. C., Fulker, D. W., & Plomin, R. (1995). Cognitive ability and academic achievement in the Colorado adoption project: A multivariate genetic analysis of parent-offspring and sibling data. *Behavior Genetics*, *25*, 1–15. http://doi.org/10.1007/BF02197237

Wainwright, M. a, Wright, M. J., Geffen, G. M., Luciano, M., & Martin, N. G. (2005). The genetic basis of academic achievement on the Queensland Core Skills Test and its shared genetic variance with IQ. *Behavior Genetics*, *35*(2), 133–45. http://doi.org/10.1007/s10519-004-1014-9

Appendices

The supplementary materials for several chapters, as references in the text, are attached as appendices

Appendix 1: Supplementary figures and tables for Chapter 2
Appendix 2: Supplementary figures and tables for Chapter 3
Appendix 3: Supplementary figures and tables for Chapter 4
Appendix 4: Supplementary tables for Chapter 6

Appendix 1: Supplementary figures and tables for Chapter 2

Supplementary information

Genetic influence on social outcomes during and after the Soviet era in Estonia

Supplementary Tables

Supplementary Table 1. EGCUT sample representativeness for educational attainment as compared to Estonian national statistics.

Supplementary Table 2. Descriptive statistics comparing the Soviet vs post-Soviet eras and males vs females for the whole EGCUT sample and when divided into historical eras using two cut-offs: (a) The post-Soviet (PS) group included participants 15 or younger when independence was regained and the Soviet (S) group included the rest of the participants; (b) The post-Soviet (PS) group included participants 10 or younger when independence was regained and the Soviet (S) group included the rest of the participants.

Supplementary Table 3. Description of cohorts for *EduYears* GWAS excluding 23andMe and EGCUT samples.

Supplementary Table 4. Testing significance of differences between correlations between GPS and SES variables across historical using two cut-offs: (a) The post-Soviet (PS) group included participants 15 or younger when independence was regained and the Soviet (S) group included the rest of the participants; (b) The post-Soviet (PS) group included participants 10 or younger when independence was regained and the Soviet (S) group included the rest of the participants.

Supplementary Table 5. Number of SNPs used to create *EduYears* GPS scores per threshold.

Supplementary Figures

Supplementary Figure 1. Variance explained by *EduYears* GPS calculated across multiple GWA study p-value thresholds for educational attainment (EA), occupational status (OS) and SES for the whole EGCUT sample and when divided into historical eras using two cut-offs: (a) The post-Soviet (PS) group included participants 15 or younger when independence was regained and the Soviet (S) group included the rest of the participants; (b) The post-Soviet (PS) group included participants 10 or younger when independence was regained and the Soviet (S) group included the rest of the participants.

Supplementary Figure 2. Variance explained by *EduYears* GPS calculated across multiple GWA study p-value thresholds when no sex correction was applied for educational attainment (EA), occupational status (OS) and SES for the whole EGCUT sample and when divided into historical eras using two cut-offs: (a) The post-Soviet (PS) group included participants 15 or younger when independence was regained and the Soviet (S) group included the rest of the participants; (b) The post-Soviet (PS) group included participants 10 or younger when independence was regained and the Soviet (S) group included the rest of the participants.

Supplementary Figure 3. Variance explained by *EduYears* GPS calculated across multiple GWA study p-value thresholds when transition time was taken into account for educational attainment (EA), occupational status (OS) and SES for historical eras using two cutoffs: (a) The post-Soviet (PS) group included participants 15 or younger when independence was regained, the Transition group included participants who were between 15-25 when independence was regained and the Soviet (S) group included the rest of the participants; (b)The post-Soviet (PS) group included participants 10 or younger when independence was regained, the Transition group included participants who were between 1-25 when independence was regained and the Soviet (S) group included the rest of the participants

Supplementary Figure 4. Variance explained by *EduYears* GPS calculated across multiple GWA study p-value thresholds for males and females separately for educational attainment (EA), occupational status (OS) and SES for the whole EGCUT sample and when divided into historical eras using two cut-offs: (a) The post-Soviet (PS) group included participants 15 or younger when independence was regained and the Soviet (S) group included the rest of the participants; (b) The post-Soviet (PS) group included participants 10 or younger when independence was regained and the Soviet (S) group included the rest of the participants.

Supplementary Figure 5. GPS heritabilities across birth cohorts for SES p-value threshold of 0.1 for a) birth cohorts across decades and b) birth cohorts when the sample was divided into 5-year intervals.

Supplementary Figure 6. Distribution of SES for the Soviet and post-Soviet groups using (a) age 15 as a cut-off and (b) age 10 as a cut-off.

Supplementary Figure 7. Distribution of *EduYears* GPS for the Soviet and post-Soviet groups using (a) age 15 as a cut-off and (b) age 10 as a cut-off.

Supplementary Figure 8. GPS heritabilities (*EduYears*) across birth cohorts for height across multiple p-value thresholds for the whole EGCUT sample and for the Soviet (S) and post-Soviet (PS) groups using (a) age 15 as a cut-off and (b) age 10 as a cut-off.

Supplementary Figure 9. SNP heritabilities (SE as error bars) for height and weight for the whole EGCUT sample and for the Soviet (S) and post-Soviet (PS) groups using the age of 15 as a cut-off. SNP heritabilities were adjusted for population stratification.

Supplementary Figure 10. Average *EduYears* GPS score (0.1 threshold) with 95% confidence intervals in (a) 10-year birth cohort bins and (b) 5-year birth cohort bins.

Supplementary Table 1. EGCUT sample representativeness for educational attainment as compared to Estonian national statistics.

	Noelementary education	Elementary education	Secondary education	High-school education	High-school education with Vocational training	Professional higher education	College/ University degree	Postgraduate degree	TOTAL
EGCUT	66	572	2714	4556	5378	825	3405	447	17963
National Statistics	3452	38947	171677	273504	181776	140285	194595	7409	1011645
EGCUT %	0.37	3.18	15.11	25.36	29.94	4.59	18.96	2.49	100.00
National Statistics %	0.34	3.85	16.97	27.04	17.97	13.87	19.24	0.73	100.00

Note: Both the National Department of Statistics and the data collected by EGCUT do not differentiate between postgraduate MSc/MA degree and doctoral degree. The National Department of statistics has a category for doctorate degree only, while there is no category for MA/MSc; EGCUT has these together as postgraduate degree

Note: High-school education with vocational training and Professional higher education are often regarded as equivalent educational qualifications by the employers.

Supplementary Table 2. Descriptive statistics comparing the Soviet vs post-Soviet eras and males vs females for the whole EGCUT sample and when divided into historical eras using two cut-offs: (a) The post-Soviet (PS) group included participants 15 or younger when independence was regained and the Soviet (S) group included the rest of the participants; (b) The post-Soviet (PS) group included participants 10 or younger when independence was regained and the Soviet (S) group included the rest of the participants.

a) Using age 15 as cut-off

	Whole sample		Soviet era		Post Soviet era		Group
	N	Mean (SD)	N	Mean (SD)	N	Mean (SD)	
Height	12494	169 .77 (9.59)	10392	169.15 (9.50)	2102	172.87 (9.40)	482.25**
Weight	12490	76.82 (17.48)	10388	77.67 (17.36)	2102	72.62 (17.46)	153.45**
Educational Attainment	12483	5.23 (1.97)	10381	5.09 (1.92)	2102	5.87 (2.06)	254.80**
Occupational Status	11419	5.41 (2.50)	9417	5.30 (2.52	2002	5.94 (2.38)	124.52**
SES	12487	(-0.03) (0.93)	10385	(-0.10)(0.92)	2102	0.25 (0.92)	242.91**

	Male		Female		Sex	Group*sex	R2
	N	Mean (SD)	N	Mean (SD)			
Height	4994	177.88 (7.43)	7500	164.37 (6.58)	6853.74**	4.42*	0.5
Weight	4993	85.37 (16.34)	7497	71.12 (15.81)	1659.00 **	33.21**	0.17
Educational Attainment	4990	5.11 (1.10)	7493	5.30 (1.95)	34.72**	8.207*	0.02
Occupational Status	4585	4.89 (2.74)	6834	5.76 (2.27)	157.48**	7.38*	0.04
SES	4991	(-0.16)(0.98)	7496	0.04 (0.88)	86.89**	0.05	0.03

Note: Group difference = F statistics; **p < 0.05. **p < 0.001; R2 = variance explained by all mean effects: group, sex and interaction between group and sex.

b) Using age 10 as cut-off

	Whole sample		Soviet era		Post Soviet era		Group
	N	Mean (SD)	N	Mean (SD)	N	Mean (SD)	
Height	12494	169 .77 (9.59)	11820	169.54 (9.55)	674	173.84 (9.34)	194.95**
Weight	12490	76.82 (17.48)	11816	77.09 (17.49)	674	72.04 (16.44)	70.95**
Educational Attainment	12483	5.23 (1.97)	11808	5.16 (1.95)	675	6.28 (2.07)	193.30**
Occupational Status	11419	5.41 (2.50)	10767	5.36 (2.51)	652	6.21 (2.35)	78.99**
SES	12487	0.03 (0.93)	11812	(-0.06) (0.93)	675	0.42 (0.91)	170.27**

	Male		Female		Sex	Group*sex	R2
	N	Mean (SD)	N	Mean (SD)			
Height	4994	177.88 (7.43)	7500	164.37 (6.58)	2492.07**	1.11	0.48
Weight	4993	85.37 (16.34)	7497	71.12 (15.81)	599.07**	5.58*	0.16
Educational Attainment	4990	5.11 (1.10)	7493	5.30 (1.95)	31.56**	12.45**	0.02
Occupational Status	4585	4.89 (2.74)	6834	5.76 (2.27)	59.79**	1.34	0.04
SES	4991	(-0.16)(0.98)	7496	0.04 (0.88)	47.90**	2.14	0.02

Note: Group difference = F statistics; **$p < 0.05$. **$p < 0.001$; R2 = variance explained by all mean effects: group, sex and interaction between group and sex.

Note: all under 25 year olds removed from the analyses

Supplementary Table 3. Description of cohorts for *EduYears* GWAS excluding 23andMe and EGCUT samples.

Study	*Full name*	*Sampling*	*Country*	*Sample size*
ACPRC	Manchester Studies of Cognitive Ageing	Population-based	England	1713
AGES	Age, Gene/ Environment Susceptibility–Reykjavik Study	Population-based	Iceland	3212
ALSPAC	Avon Longitudinal Study of Parents and Children	Population-based birth cohort	England	2877
ASPS	Austrian Stroke Prevention Study	Population-based	Austria	777
BASE-II	Berlin Aging Study II	Population-based	Germany	1619
CoLaus	Cohorte Lausannoise	Population-based	Switzerland	3269
COPSAC2000	Copenhagen Studies on Asthma in Childhood 2000	Case-control birth cohort	Germany	318
CROATIA-Korčula	Croatia Korčula	Population-based (Isolate)	Croatia	842

deCODE	deCODE genetics	Population-based	Iceland	46758
DHS	Dortmund Health Study	Population-based	Germany	953
DIL	Wellcome Trust Diabetes and Inflammation Laboratory	Population-based	England	2578
ERF	Erasmus Rucphen Family Study	Family-based	Netherlands	2433
FamHS	Family Heart Study	Family-based	USA	3483
FINRISK	The National FINRISK Study	Case-control (Cardiovascular health)	Finland	1685
FTC	Finnish Twin Cohort	Family-based	Finland	2418
GOYA	Genetics of Overweight Young Adults	Case-control (Obesity)	Denmark	1459
GRAPHIC	Genetic Regulation of Arterial Pressure in Humans	Population-based	England	727
GS	Generation Scotland	Population-based	Scotland	8776

H2000 Cases	Health 2000	Case-control (Metabolic syndrome)	Finland	797
H2000 Controls	Same as above	Case-control (Metabolic syndrome)	Finland	819
HBCS	Helsinki Birth Cohort Study	Population-based birth cohort	Finland	1617
HCS	Hunter Community Study	Population-based	Australia	1946
HNRS (CorexB)	Heinz Nixdorf Recall Study	Population-based	Germany	1401
HNRS (Oexpr)	Same as above	Same as above	Germany	1347
HNRS (Omni1)	Same as above	Same as above	Germany	778
HRS	Health and Retirement Study	Population-based	USA	9963
Hypergenes	Hypergenes	Case-control	Italy/ UK/ Belgium	815

INGI-CARL	Italian Network of Genetic Isolates - Carlantino	Population-based (Isolate)	Italy	947
INGI-FVG	Italian Network of Genetic Isolates - Friuli Venezia Giulia	Population-based (Isolate)	Italy	943
KORA S3	Kooperative Gesundheitsforschung in der Region Augsburg	Population-based	Germany	2655
KORA S4	Same as above	Population-based	Germany	2721
LBC1921	Lothian Birth Cohort 1921	Population-based birth cohort	Scotland	515
LBC1936	Lothian Birth Cohort 1936	Population-based birth cohort	Scotland	1003
LifeLines	The LifeLines Cohort Study	Population-based	Netherlands	12539
MCTFR	Minnesota Center for Twin and Family Research	Family-based, but only founders used.	USA	3819
MGS	Molecular Genetics of Schizophrenia	Population-based	USA	2313

MoBa	Mother and Child Cohort of NIPH	Population-based (Nested case-control)	Norway	622
NBS	Nijmegen Biomedical Study	Population-based	Netherlands	1808
NESDA	Netherlands Study of Depression and Anxiety	Case-control (Mental health)	Netherlands	1820
NFBC66	Northern Finland Birth Cohort 1966	Population-based	Finland	5297
NTR	Netherlands Twin Register	Family-based	Netherlands	5246
OGP	Ogliastra Genetic Park	Population-based	Italy	370
OGP-Talana	Ogliastra Genetic Park-Talana	Population-based (Isolate)	Italy	544
ORCADES	Orkney Complex Disease Study	Population-based (Isolate)	Scotland	1828
PREVEND	Prevention of Renal and Vascular End-stage Disease	Population-based	Netherlands	3578
QIMR	Queensland Institute of Medical Research	Family-based	Australia	8006

RS-I	Rotterdam Study Baseline	Population-based	Netherlands	6108
RS-II	Rotterdam Study Extension of Baseline	Same as above	Netherlands	1667
RS-III	Rotterdam Study Young	Same as above	Netherlands	3040
Rush-MAP	Rush University Medical Center - Memory and Aging Project	Community-based	USA	887
Rush-ROS	Rush University Medical Center - Religious Orders Study	Community-based	USA	808
SardiNIA	SardiNIA Study of Aging	Family-based	Italy	5616
SHIP	Study of Health in Pomerania	Population-based	Germany	3556
SHIP-TREND	Study of Health in Pomerania	Population-based	Germany	901
STR – Salty	Swedish Twin Registry	Family-based	Sweden	4832
STR – Twingene	Swedish Twin Registry	Family-based	Sweden	9553

THISEAS	The Hellenic Study of Interactions between SNPs & Eating in Atherosclerosis Susceptibility	Case-control	Greece	829
TwinsUK	St Thomas' UK Adult Twin Registry	Population-based	England	4012
WTCCC58C	1958 British Birth Cohort	Population-based	England	2804
YFS	The Cardiovascular Risk in Young Finns Study	Population-based	Finland	2029

Note: Adapted from Okbay et al. 2016 (see Okbay et al. 2016 for further details)

Supplementary Table 4. Testing significance of differences between correlations between GPS and SES variables across historical using two cut-offs: (a) The post-Soviet (PS) group included participants 15 or younger when independence was regained and the Soviet (S) group included the rest of the participants; (b) The post-Soviet (PS) group included participants 10 or younger when independence was regained and the Soviet (S) group included the rest of the participants.

	Z	p-value
a)		
rOccupation Soviet-rOccupation post Soviet	1.43	0.153
rEducational Attainment Soviet- rEducational Attainment post Soviet	1.78	0.075
rSES Soviet- rSES post Soviet	2.38	0.017
b)		
rOccupation Soviet-rOccupation post Soviet	5.29	<0.001
rEducational Attainment Soviet- rEducational Attainment post Soviet	5.5	<0.001
rSES Soviet- rSES post Sovet	6.46	<0.001

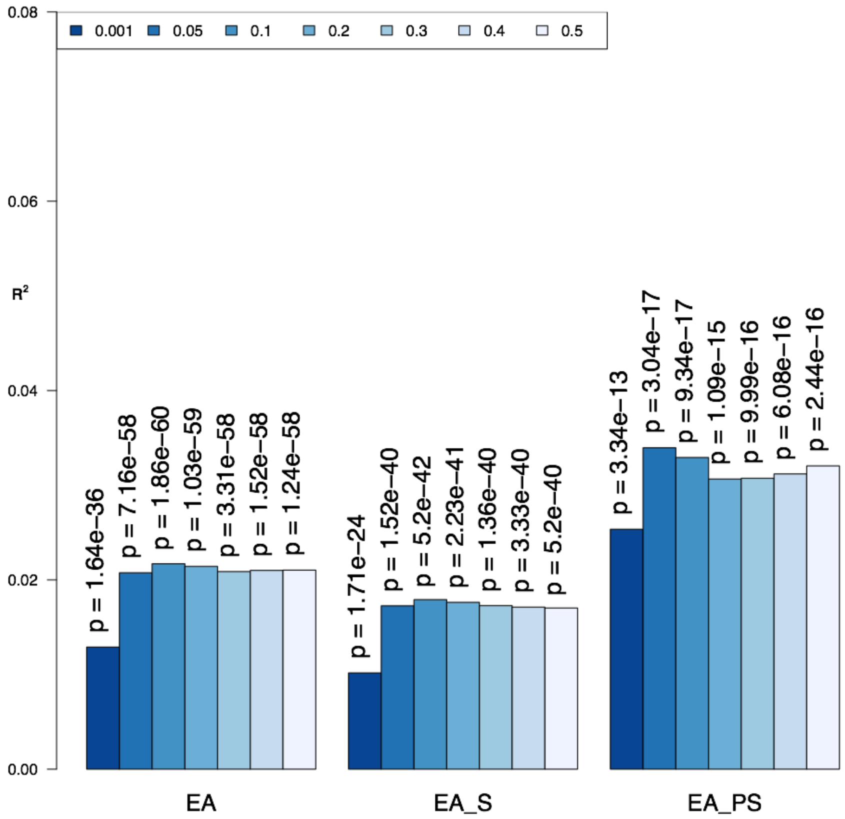
Note: *r*= Pearson correlation; Z = Fisher r-to-z transformation to assess significance of difference between correlation coefficients.

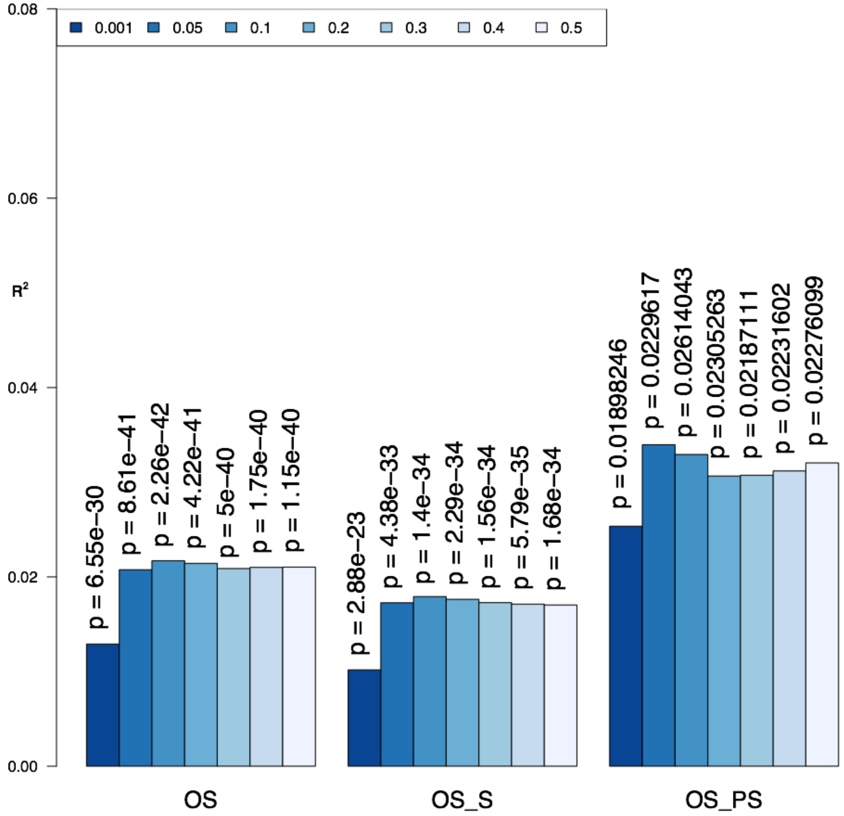
Supplementary Table 5. Number of SNPs used to create *EduYears* GPS scores per threshold.

p-value threshold	Number of SNPs
0.001	1987
0.05	19575
0.1	30944
0.2	48864
0.3	63280
0.4	75526
0.5	85889

Supplementary Figure 1. Variance explained by *EduYears* GPS calculated across multiple GWA study p-value thresholds for educational attainment (EA), occupational status (OS) and SES for the whole EGCUT sample and when divided into historical eras using two cut-offs: (a) The post-Soviet (PS) group included participants 15 or younger when independence was regained and the Soviet (S) group included the rest of the participants; (b) The post-Soviet (PS) group included participants 10 or younger when independence was regained and the Soviet (S) group included the rest of the participants.

a) Age 15 as cut-off




0.001
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0.1
0.2
0.3
0.4
0.5
0.08
0.06
0.04
0.02
0.00
R^2
p = 6.55e−30
p = 8.61e−41
p = 2.26e−42
p = 4.22e−41
p = 5e−40
p = 1.75e−40
p = 1.15e−40
p = 2.88e−23
p = 4.38e−33
p = 1.4e−34
p = 2.29e−34
p = 1.56e−34
p = 5.79e−35
p = 1.68e−34
p = 0.01898246
p = 0.0229617
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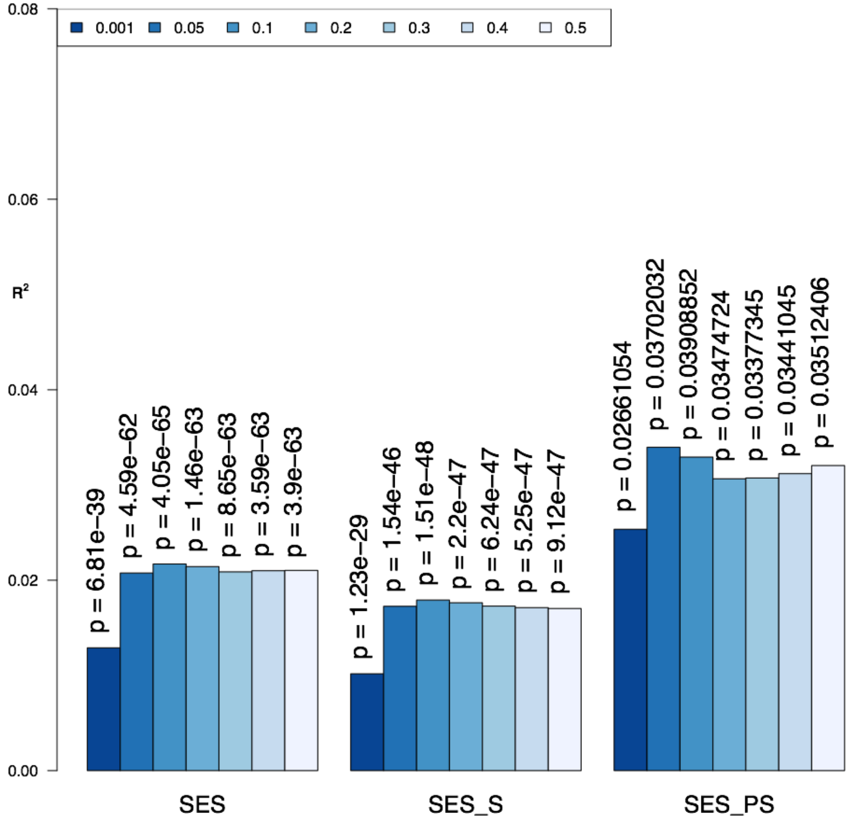
OS
OS_S
OS_PS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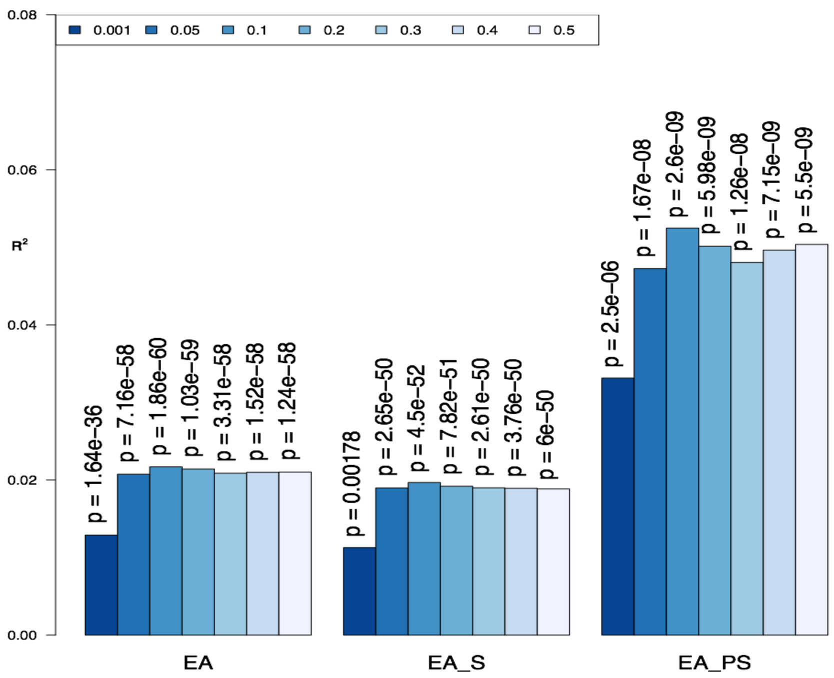
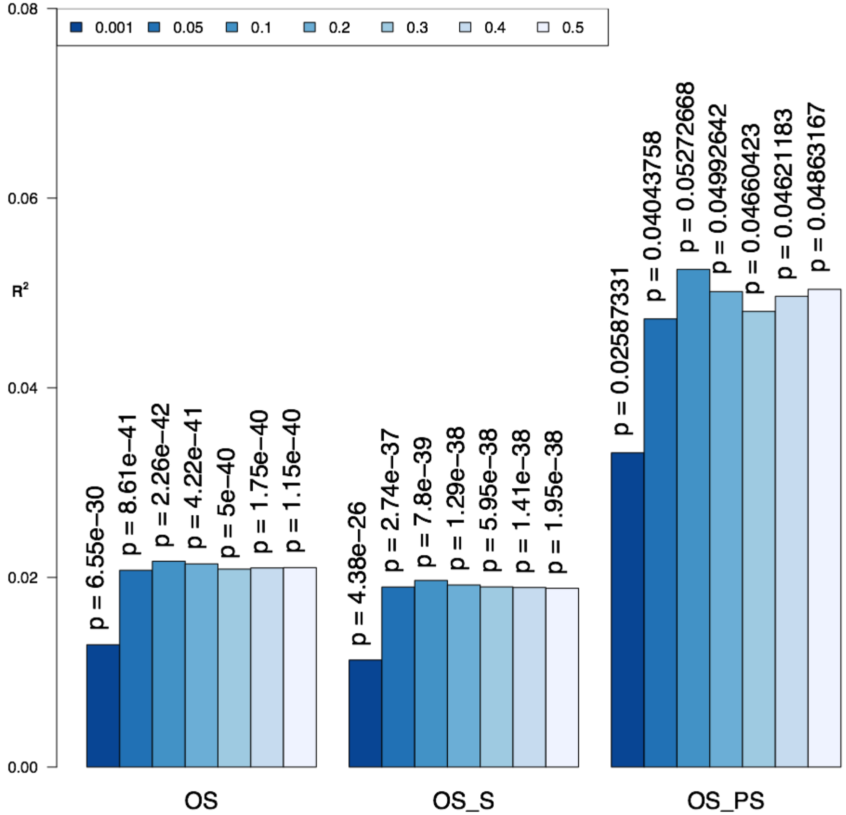
0.1
0.2
0.3
0.4
0.5
0.08
0.06
0.04
0.02
0.00
R²
p = 6.81e−39
p = 4.59e−62
p = 4.05e−65
p = 1.46e−63
p = 8.65e−63
p = 3.59e−63
p = 3.9e−63
p = 1.23e−29
p = 1.54e−46
p = 1.51e−48
p = 2.2e−47
p = 6.24e−47
p = 5.25e−47
p = 9.12e−47
p = 0.02661054
p = 0.03702032
p = 0.03908852
p = 0.03474724
p = 0.03377345
p = 0.03441045
p = 0.03512406
SES
SES_S
SES_PS

b) Age 10 as cut-off




0.08
0.06
0.04
0.02
0.00
R²
0.001
0.05
0.1
0.2
0.3
0.4
0.5
p = 6.55e−30
p = 8.61e−41
p = 2.26e−42
p = 4.22e−41
p = 5e−40
p = 1.75e−40
p = 1.15e−40
p = 4.38e−26
p = 2.74e−37
p = 7.8e−39
p = 1.29e−38
p = 5.95e−38
p = 1.41e−38
p = 1.95e−38
p = 0.02587331
p = 0.04043758
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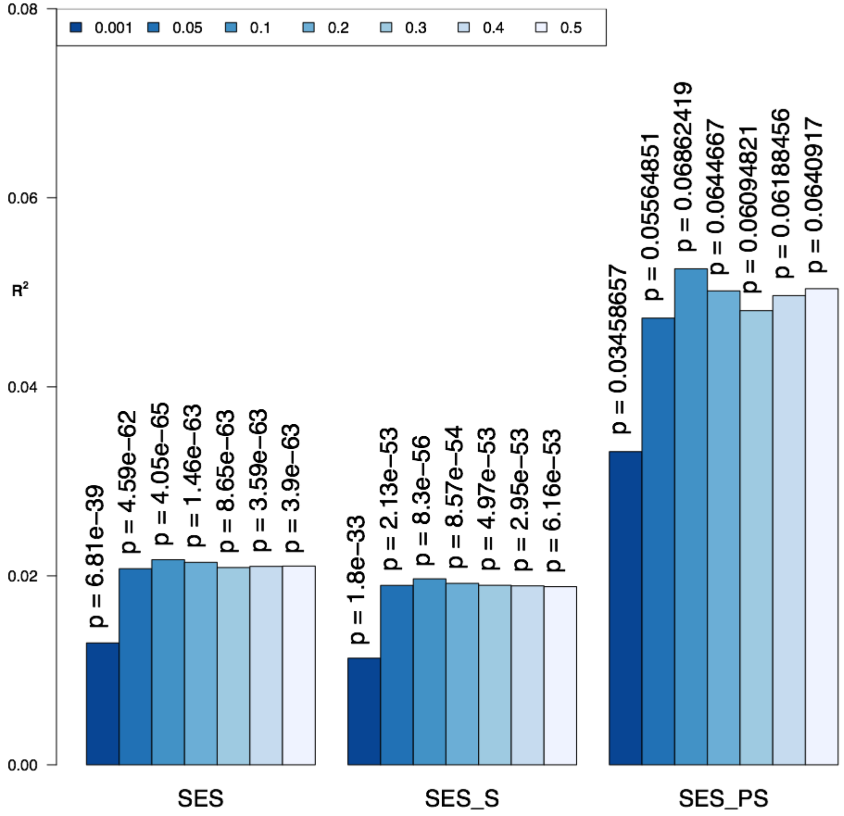
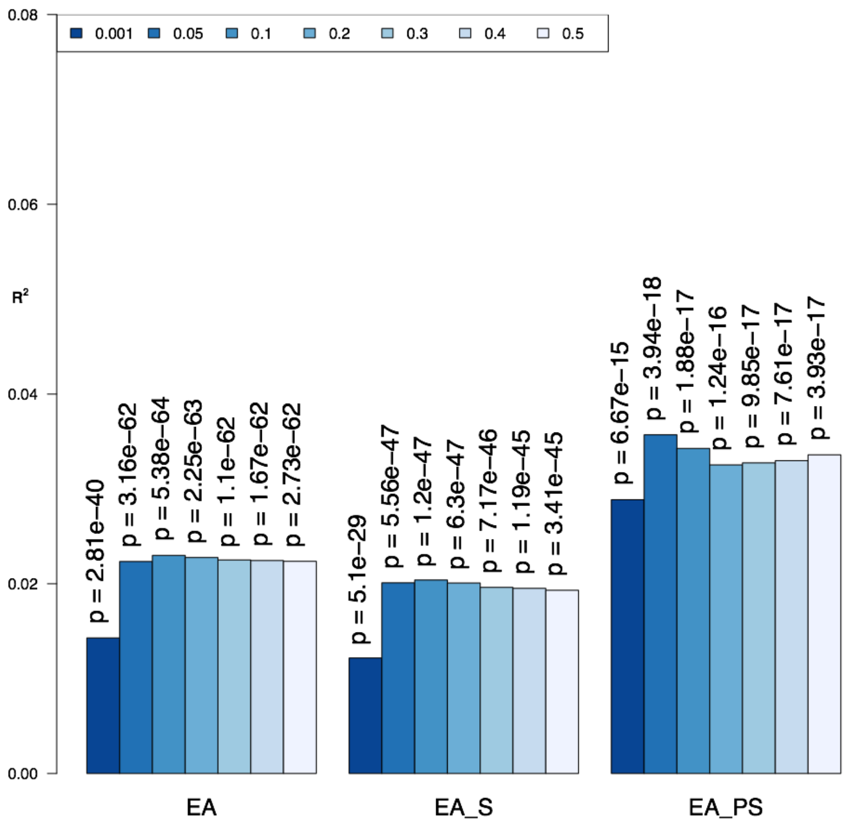
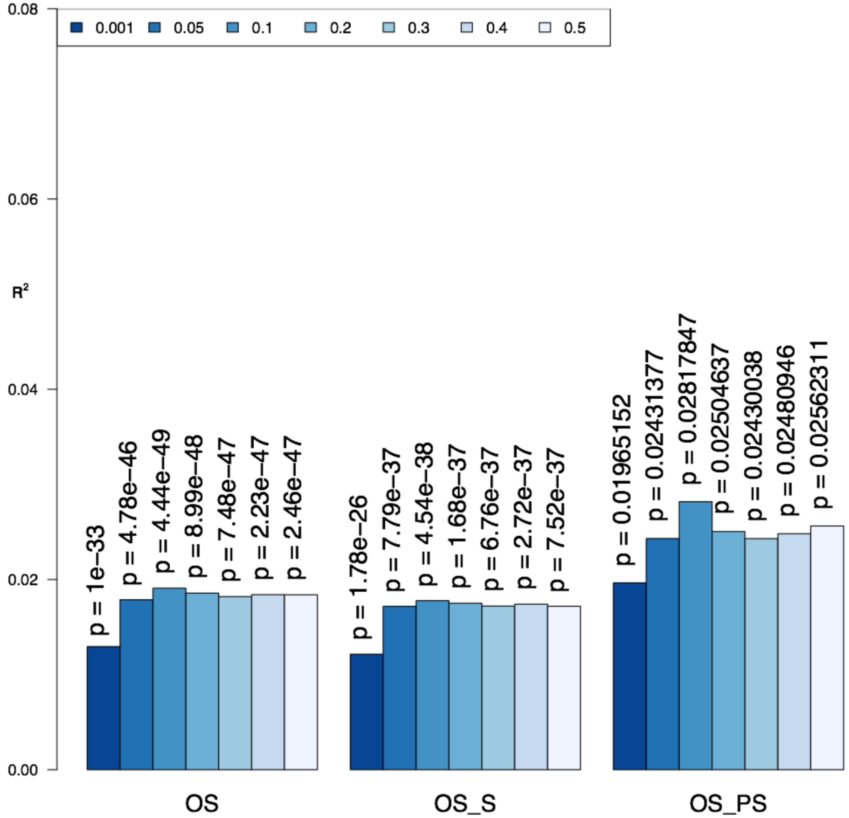
p = 0.04863167
OS
OS_S
OS_PS

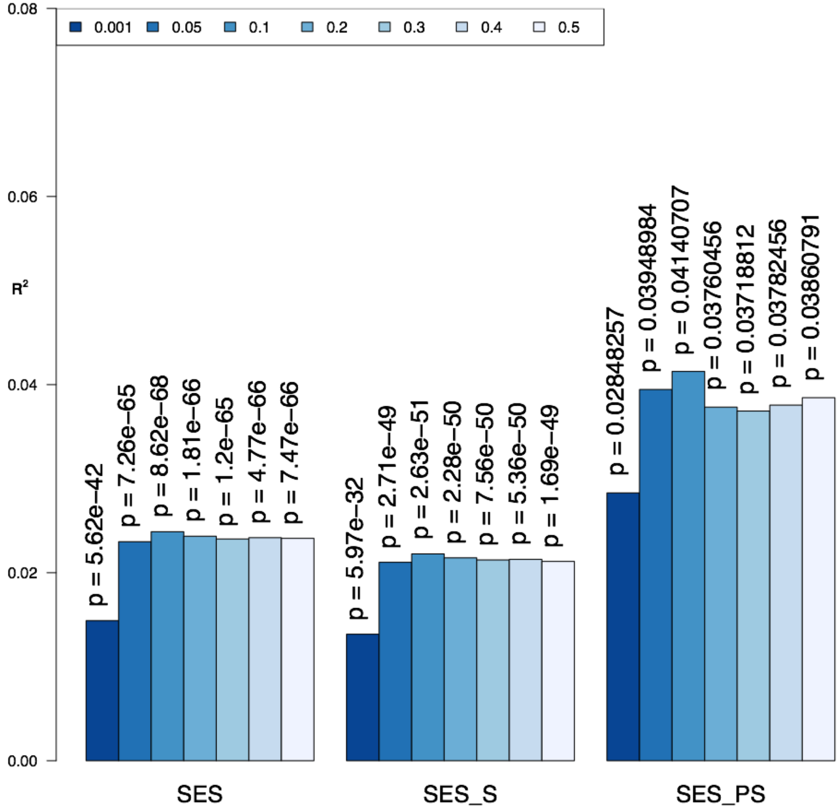

0.08
0.06
0.04
0.02
0.00
R^2
0.001
0.05
0.1
0.2
0.3
0.4
0.5
p = 6.81e−39
p = 4.59e−62
p = 4.05e−65
p = 1.46e−63
p = 8.65e−63
p = 3.59e−63
p = 3.9e−63
p = 1.8e−33
p = 2.13e−53
p = 8.3e−56
p = 8.57e−54
p = 4.97e−53
p = 2.95e−53
p = 6.16e−53
p = 0.03458657
p = 0.05564851
p = 0.06862419
p = 0.0644667
p = 0.06094821
p = 0.06188456
p = 0.0640917
SES
SES_S
SES_PS

Supplementary Figure 2. Variance explained by *EduYears* GPS calculated across multiple GWA study p-value thresholds when no sex correction was applied for educational attainment (EA), occupational status (OS) and SES for the whole EGCUT sample and when divided into historical eras using two cut-offs: (a) The post-Soviet (PS) group included participants 15 or younger when independence was regained and the Soviet (S) group included the rest of the participants; (b) The post-Soviet (PS) group included participants 10 or younger when independence was regained and the Soviet (S) group included the rest of the participants.

a)




0.08
0.06
0.04
0.02
0.00
R^2
0.001
0.05
0.1
0.2
0.3
0.4
0.5
p = 1e−33
p = 4.78e−46
p = 4.44e−49
p = 8.99e−48
p = 7.48e−47
p = 2.23e−47
p = 2.46e−47
p = 1.78e−26
p = 7.79e−37
p = 4.54e−38
p = 1.68e−37
p = 6.76e−37
p = 2.72e−37
p = 7.52e−37
p = 0.01965152
p = 0.02431377
p = 0.02817847
p = 0.02504637
p = 0.02430038
p = 0.02480946
p = 0.02562311
OS
OS_S
OS_PS



0.08
0.06
0.04
0.02
0.00
R²
0.001
0.05
0.1
0.2
0.3
0.4
0.5
p = 5.62e−42
p = 7.26e−65
p = 8.62e−68
p = 1.81e−66
p = 1.2e−65
p = 4.77e−66
p = 7.47e−66
p = 5.97e−32
p = 2.71e−49
p = 2.63e−51
p = 2.28e−50
p = 7.56e−50
p = 5.36e−50
p = 1.69e−49
p = 0.02848257
p = 0.03948984
p = 0.04140707
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p = 0.03718812
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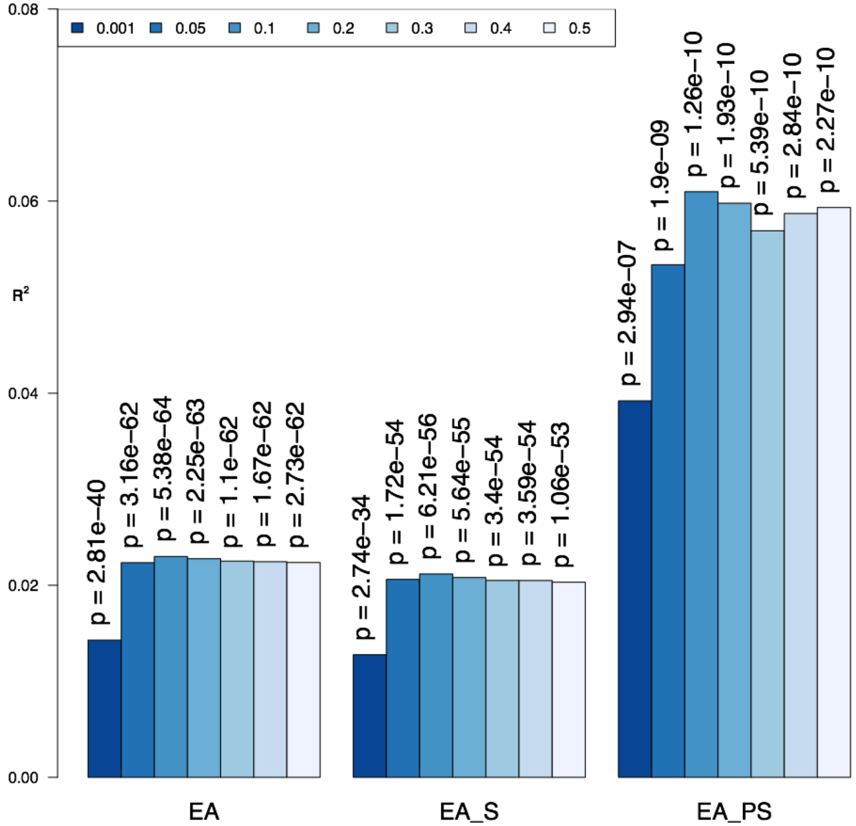
SES
SES_S
SES_PS

b)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0.2
0.3
0.4
0.5
0.08
0.06
0.04
0.02
0.00
R²
p = 2.81e−40
p = 3.16e−62
p = 5.38e−64
p = 2.25e−63
p = 1.1e−62
p = 1.67e−62
p = 2.73e−62
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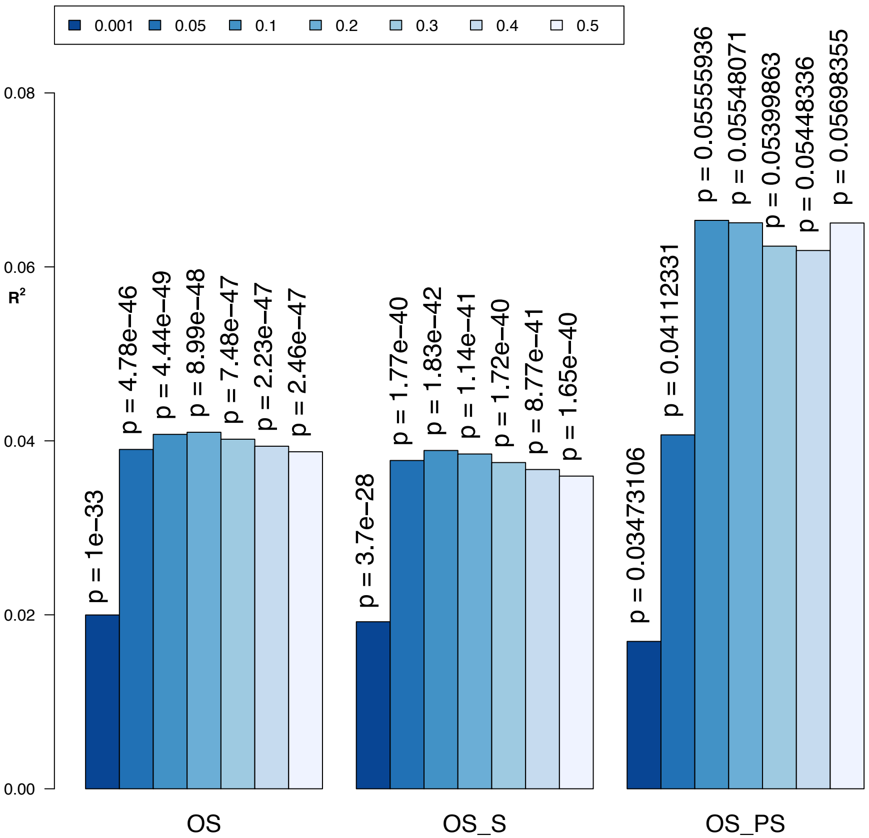
EA
EA_S
EA_PS



0.001
0.05
0.1
0.2
0.3
0.4
0.5
0.08
0.06
0.04
0.02
0.00
R^2
p = 1e−33
p = 4.78e−46
p = 4.44e−49
p = 8.99e−48
p = 7.48e−47
p = 2.23e−47
p = 2.46e−47
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p = 1.83e−42
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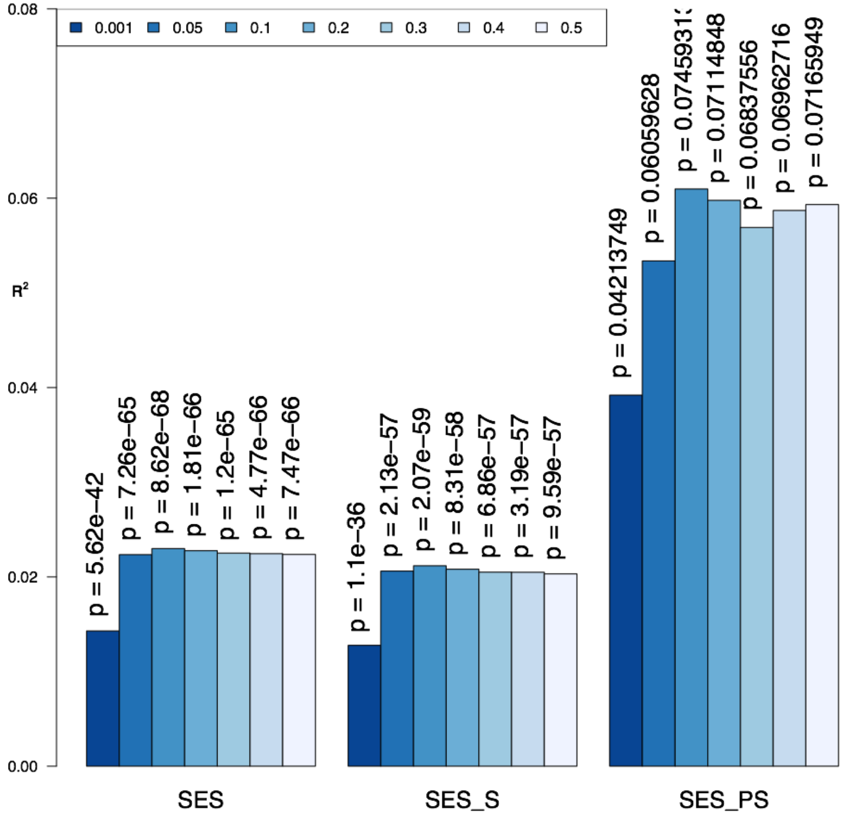
OS_S
OS_PS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0.2
0.3
0.4
0.5
R²
0.00
0.02
0.04
0.06
0.08
p = 5.62e−42
p = 7.26e−65
p = 8.62e−68
p = 1.81e−66
p = 1.2e−65
p = 4.77e−66
p = 7.47e−66
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p = 9.59e−57
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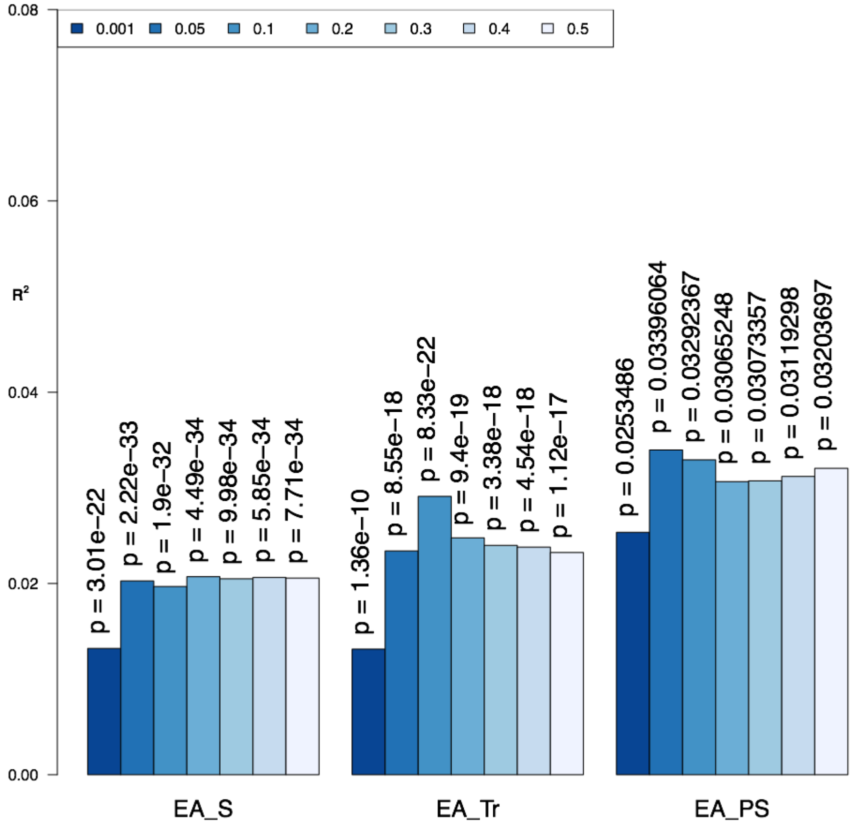
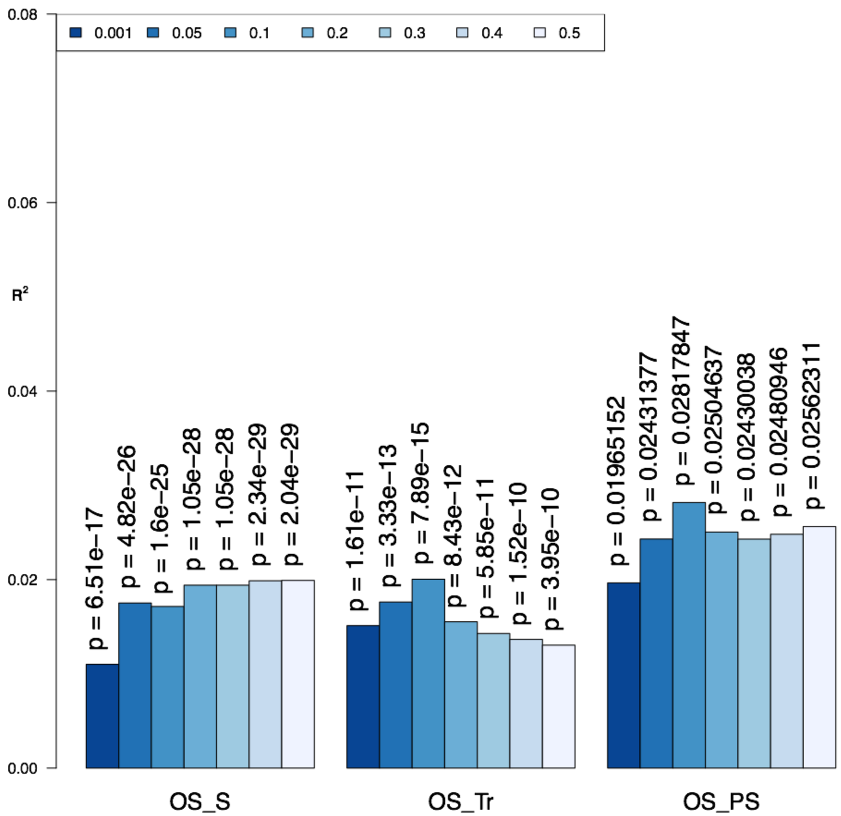
p = 0.06059628
p = 0.0745931
p = 0.07114848
p = 0.06837556
p = 0.06962716
p = 0.07165949
SES
SES_S
SES_PS

Supplementary Figure 3. Variance explained by *EduYears* GPS calculated across multiple GWA study p-value thresholds when transition time was taken into account for educational attainment (EA), occupational status (OS) and SES for historical eras using two cutoffs: (a) The post-Soviet (PS) group included participants 15 or younger when independence was regained, the Transition group included participants who were between 15-25 when independence was regained and the Soviet (S) group included the rest of the participants; (b)The post-Soviet (PS) group included participants 10 or younger when independence was regained, the Transition group included participants who were between 1-25 when independence was regained and the Soviet (S) group included the rest of the participants

a)





0.001
0.05
0.1
0.2
0.3
0.4
0.5
R^2
0.08
0.06
0.04
0.02
0.00
p = 6.51e−17
p = 4.82e−26
p = 1.6e−25
p = 1.05e−28
p = 1.05e−28
p = 2.34e−29
p = 2.04e−29
p = 1.61e−11
p = 3.33e−13
p = 7.89e−15
p = 8.43e−12
p = 5.85e−11
p = 1.52e−10
p = 3.95e−10
p = 0.01965152
p = 0.02431377
p = 0.02817847
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p = 0.02430038
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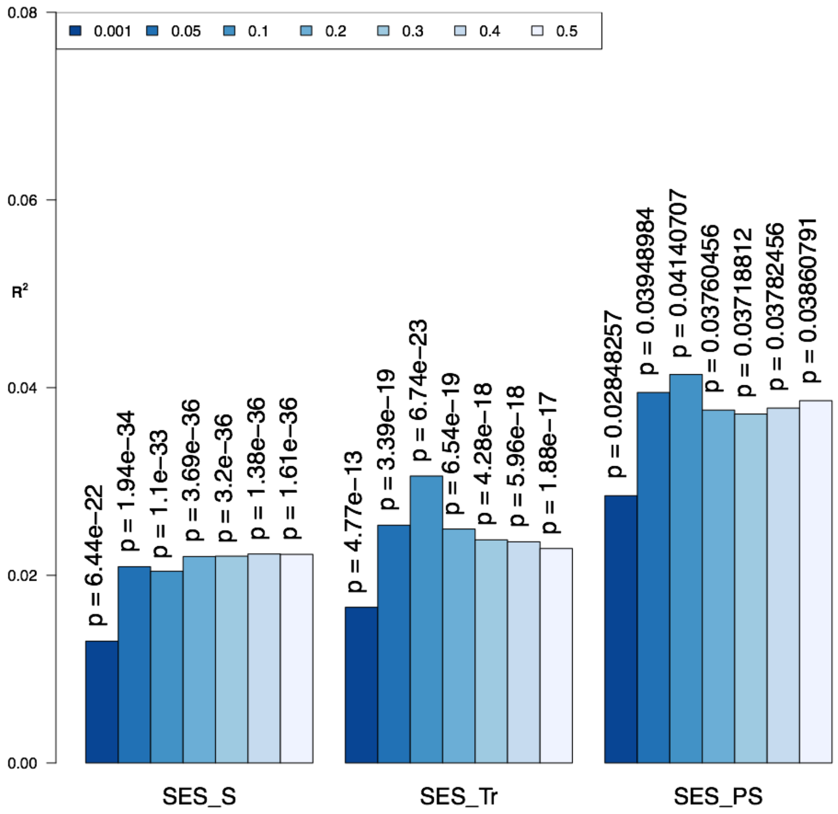
p = 0.02562311
OS_S
OS_Tr
OS_PS


0.08
0.06
0.04
0.02
0.00
R²
0.001
0.05
0.1
0.2
0.3
0.4
0.5
p = 6.44e−22
p = 1.94e−34
p = 1.1e−33
p = 3.69e−36
p = 3.2e−36
p = 1.38e−36
p = 1.61e−36
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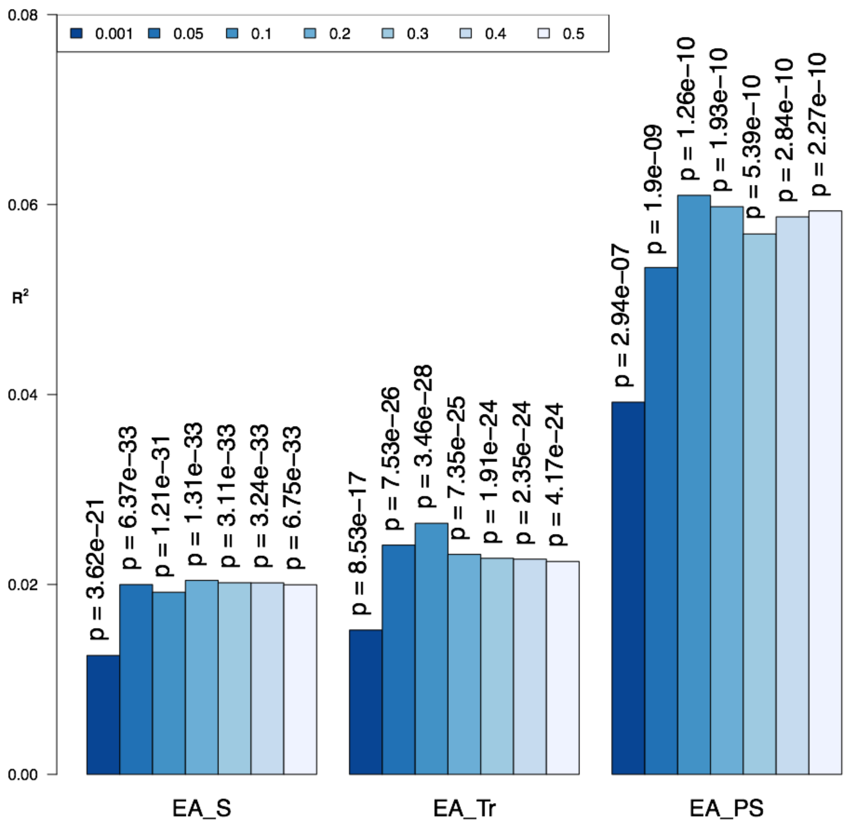
p = 6.54e−19
p = 4.28e−18
p = 5.96e−18
p = 1.88e−17
p = 0.02848257
p = 0.03948984
p = 0.04140707
p = 0.03760456
p = 0.03718812
p = 0.03782456
p = 0.03860791
SES_S
SES_Tr
SES_PS

b)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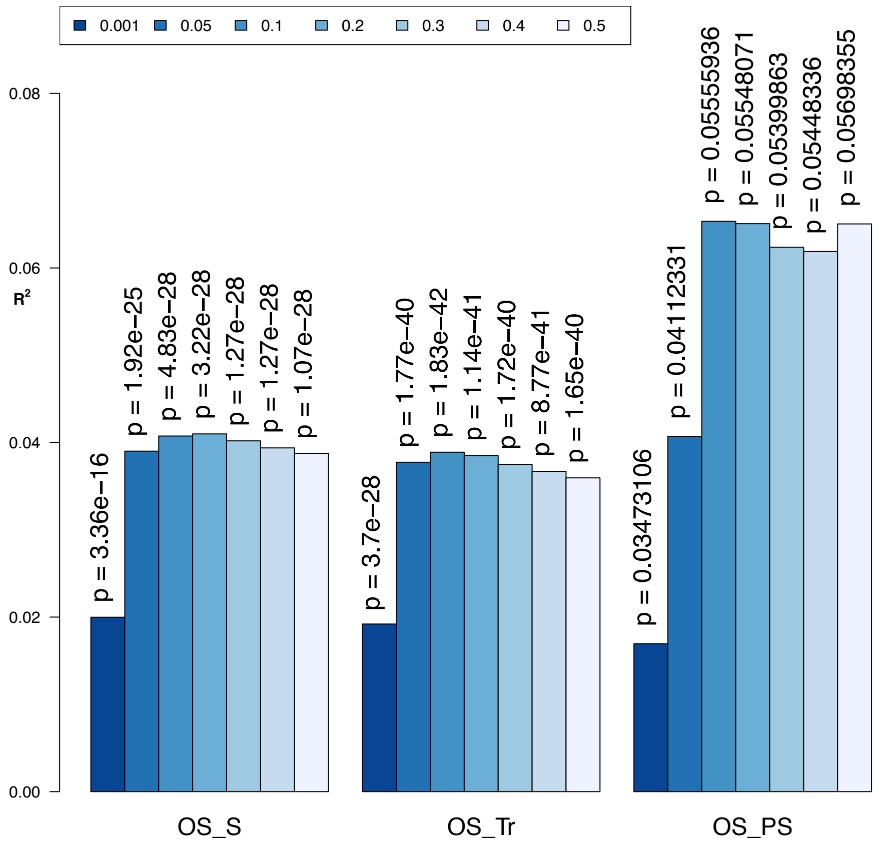
0.3
0.4
0.5
0.08
0.06
0.04
0.02
0.00
R²
p = 3.62e−21
p = 6.37e−33
p = 1.21e−31
p = 1.31e−33
p = 3.11e−33
p = 3.24e−33
p = 6.75e−33
p = 8.53e−17
p = 7.53e−26
p = 3.46e−28
p = 7.35e−25
p = 1.91e−24
p = 2.35e−24
p = 4.17e−24
p = 2.94e−07
p = 1.9e−09
p = 1.26e−10
p = 1.93e−10
p = 5.39e−10
p = 2.84e−10
p = 2.27e−10
EA_S
EA_Tr
EA_PS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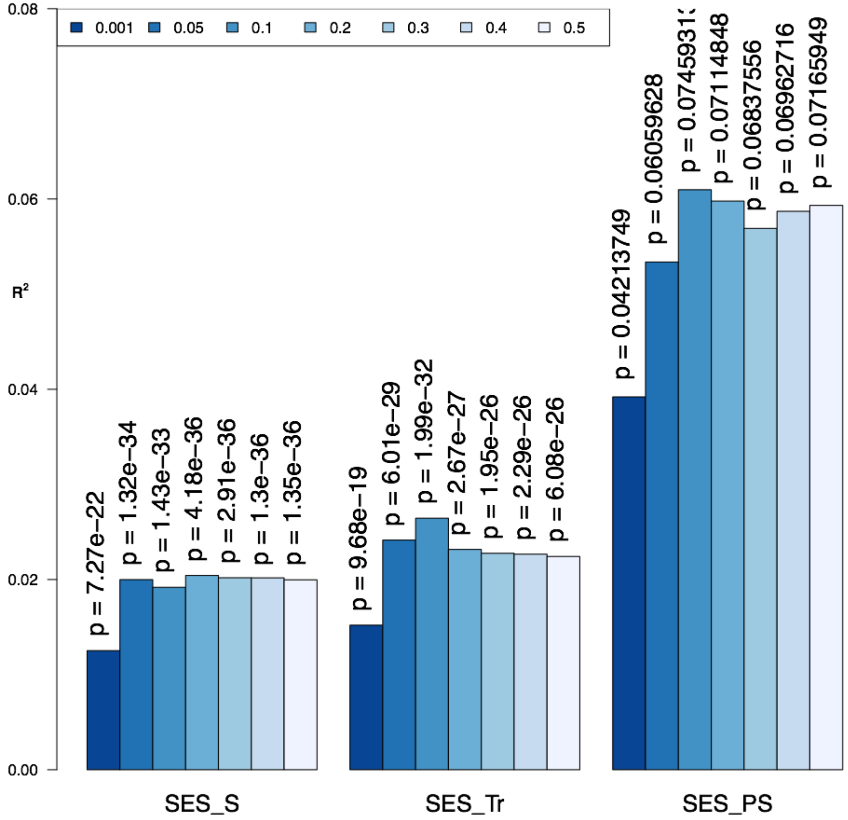
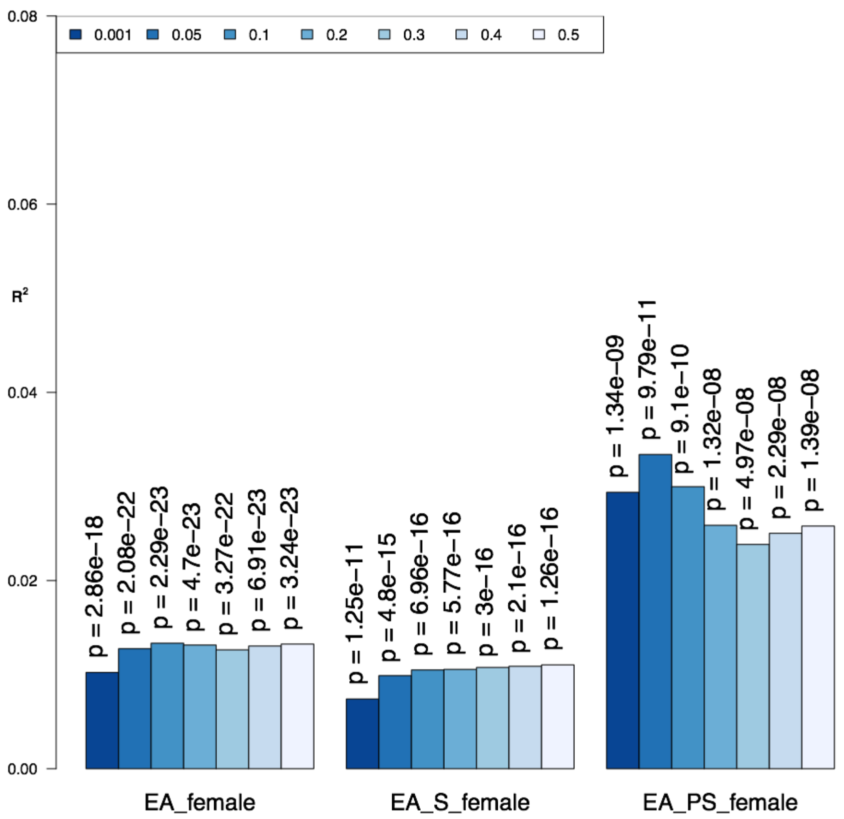
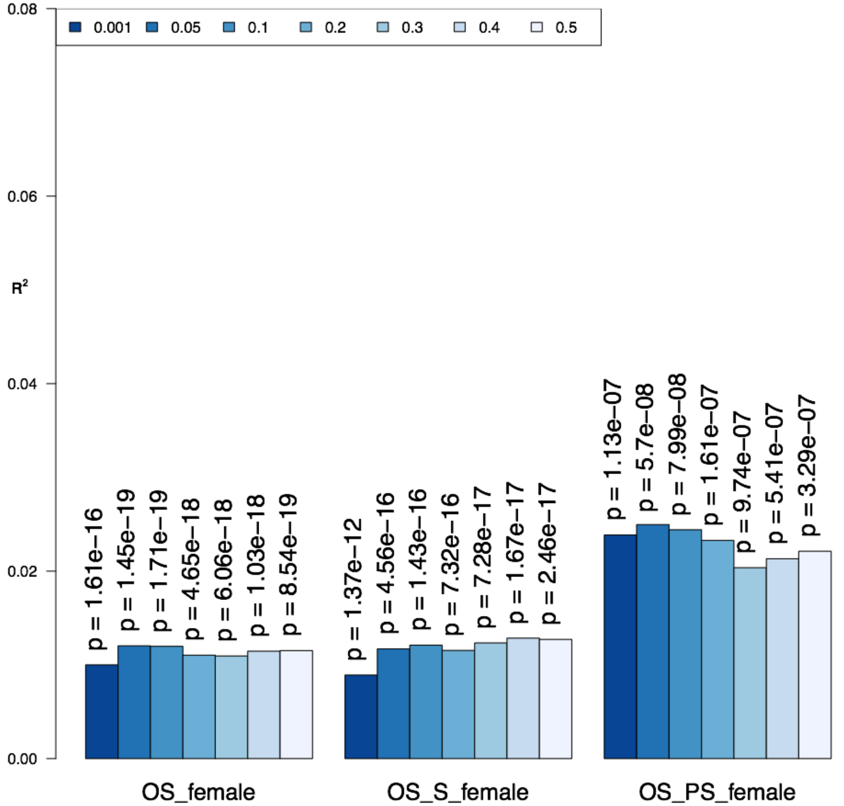
0.05
0.1
0.2
0.3
0.4
0.5
R²
0.00
0.02
0.04
0.06
0.08
p = 3.36e−16
p = 1.92e−25
p = 4.83e−28
p = 3.22e−28
p = 1.27e−28
p = 1.27e−28
p = 1.07e−28
p = 3.7e−28
p = 1.77e−40
p = 1.83e−42
p = 1.14e−41
p = 1.72e−40
p = 8.77e−41
p = 1.65e−40
p = 0.03473106
p = 0.04112331
p = 0.05555936
p = 0.05548071
p = 0.05399863
p = 0.05448336
p = 0.05698355
OS_S
OS_Tr
OS_PS

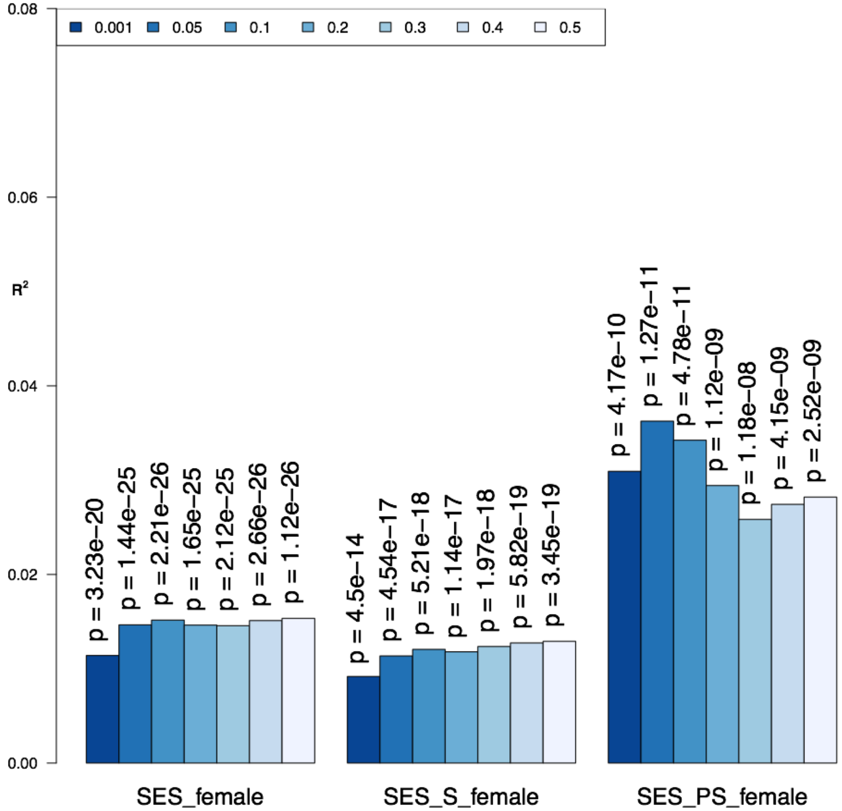

0.08
0.06
0.04
0.02
0.00
R²
0.001
0.05
0.1
0.2
0.3
0.4
0.5
p = 7.27e−22
p = 1.32e−34
p = 1.43e−33
p = 4.18e−36
p = 2.91e−36
p = 1.3e−36
p = 1.35e−36
p = 9.68e−19
p = 6.01e−29
p = 1.99e−32
p = 2.67e−27
p = 1.95e−26
p = 2.29e−26
p = 6.08e−26
p = 0.04213749
p = 0.06059628
p = 0.07114848
p = 0.06837556
p = 0.06962716
p = 0.07165949
SES_S
SES_Tr
SES_PS

Supplementary Figure 4. Variance explained by *EduYears* GPS calculated across multiple GWA study p-value thresholds for males and females separately for educational attainment (EA), occupational status (OS) and SES for the whole EGCUT sample and when divided into historical eras using two cut-offs: (a) The post-Soviet (PS) group included participants 15 or younger when independence was regained and the Soviet (S) group included the rest of the participants; (b) The post-Soviet (PS) group included participants 10 or younger when independence was regained and the Soviet (S) group included the rest of the participants.

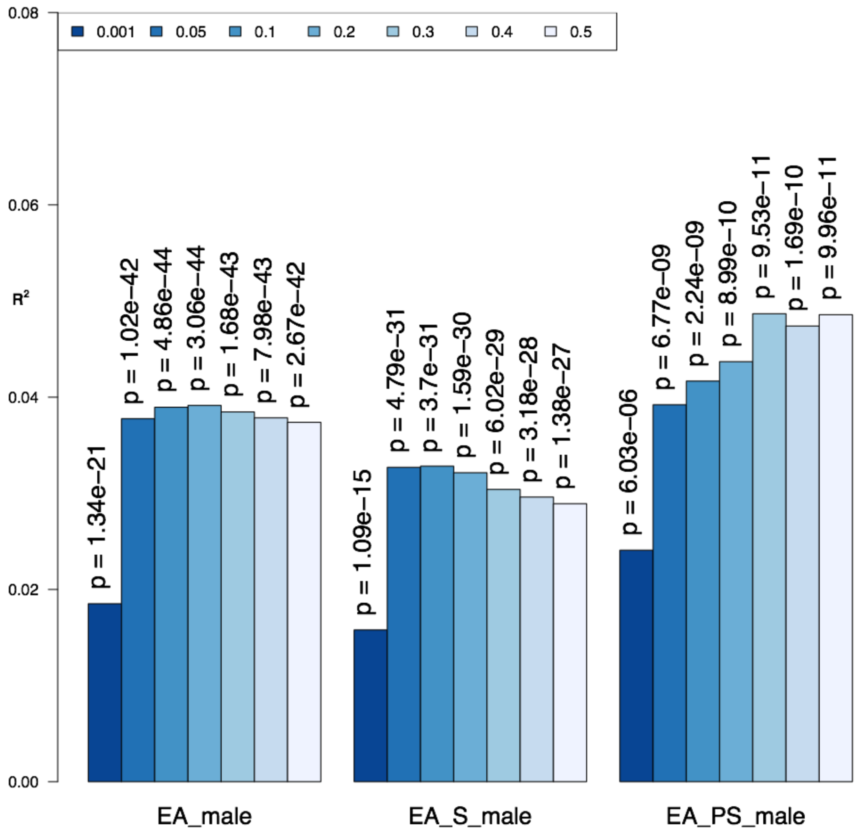
a) **Females**

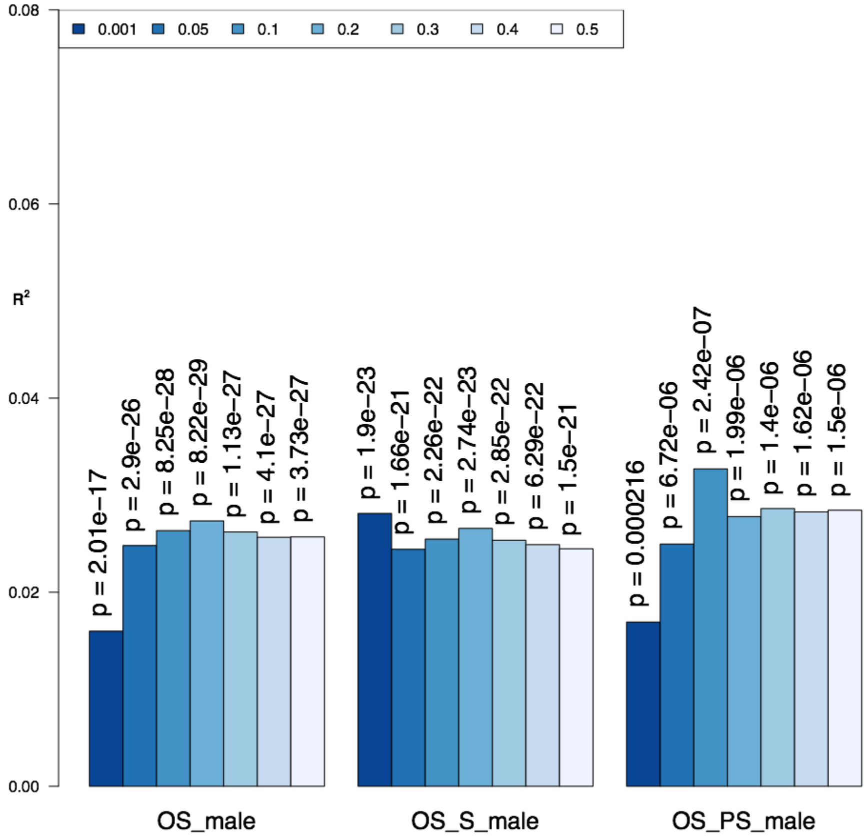



0.08
0.06
0.04
0.02
0.00
R²
0.001
0.05
0.1
0.2
0.3
0.4
0.5
p = 1.61e−16
p = 1.45e−19
p = 1.71e−19
p = 4.65e−18
p = 6.06e−18
p = 1.03e−18
p = 8.54e−19
p = 1.37e−12
p = 4.56e−16
p = 1.43e−16
p = 7.32e−16
p = 7.28e−17
p = 1.67e−17
p = 2.46e−17
p = 1.13e−07
p = 5.7e−08
p = 7.99e−08
p = 1.61e−07
p = 9.74e−07
p = 5.41e−07
p = 3.29e−07
OS_female
OS_S_female
OS_PS_female

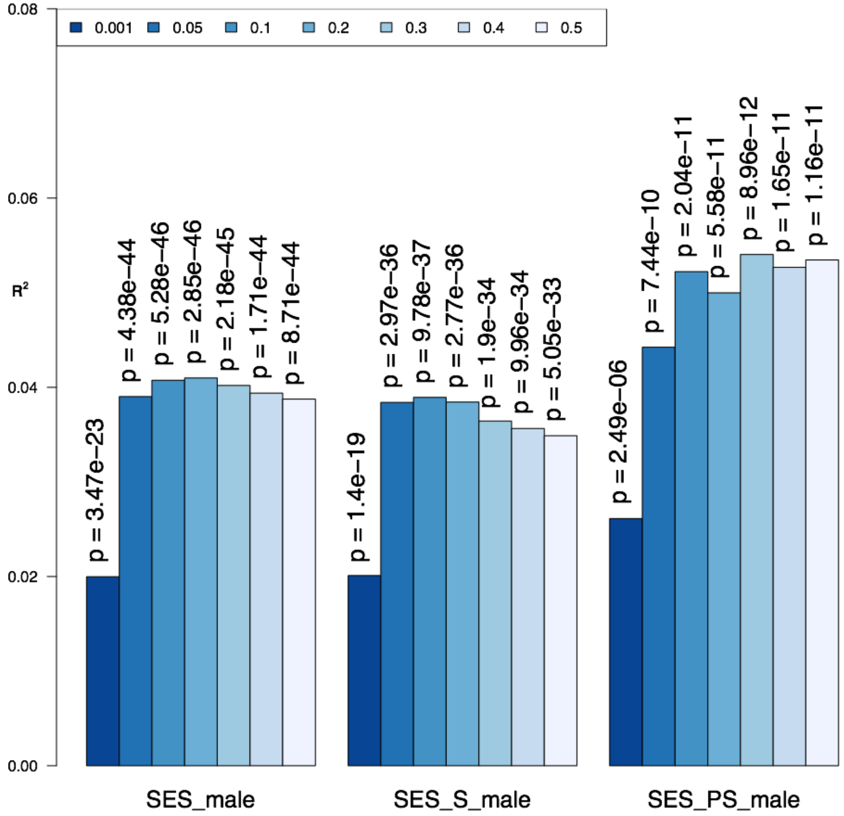

0.001
0.05
0.1
0.2
0.3
0.4
0.5
0.08
0.06
R^2
0.04
0.02
0.00
p = 3.23e−20
p = 1.44e−25
p = 2.21e−26
p = 1.65e−25
p = 2.12e−25
p = 2.66e−26
p = 1.12e−26
p = 4.5e−14
p = 4.54e−17
p = 5.21e−18
p = 1.14e−17
p = 1.97e−18
p = 5.82e−19
p = 3.45e−19
p = 4.17e−10
p = 1.27e−11
p = 4.78e−11
p = 1.12e−09
p = 1.18e−08
p = 4.15e−09
p = 2.52e−09
SES_female
SES_S_female
SES_PS_female

Males


0.08
0.06
0.04
0.02
0.00
R²
0.001
0.05
0.1
0.2
0.3
0.4
0.5
p = 1.34e−21
p = 1.02e−42
p = 4.86e−44
p = 3.06e−44
p = 1.68e−43
p = 7.98e−43
p = 2.67e−42
p = 1.09e−15
p = 4.79e−31
p = 3.7e−31
p = 1.59e−30
p = 6.02e−29
p = 3.18e−28
p = 1.38e−27
p = 6.03e−06
p = 6.77e−09
p = 2.24e−09
p = 8.99e−10
p = 9.53e−11
p = 1.69e−10
p = 9.96e−11
EA_male
EA_S_male
EA_PS_male



0.001
0.05
0.1
0.2
0.3
0.4
0.5
0.08
0.06
R^2
0.04
0.02
0.00
p = 2.01e−17
p = 2.9e−26
p = 8.25e−28
p = 8.22e−29
p = 1.13e−27
p = 4.1e−27
p = 3.73e−27
p = 1.9e−23
p = 1.66e−21
p = 2.26e−22
p = 2.74e−23
p = 2.85e−22
p = 6.29e−22
p = 1.5e−21
p = 0.000216
p = 6.72e−06
p = 2.42e−07
p = 1.99e−06
p = 1.4e−06
p = 1.62e−06
p = 1.5e−06
OS_male
OS_S_male
OS_PS_male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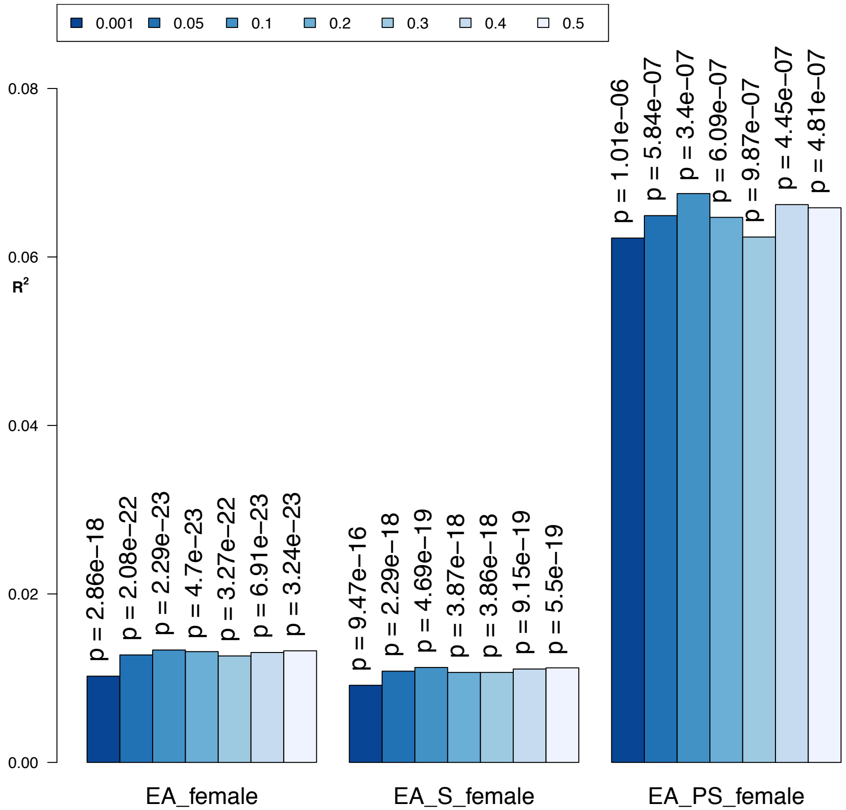
0.06
0.04
0.02
0.00
R²
0.001
0.05
0.1
0.2
0.3
0.4
0.5
p = 3.47e−23
p = 4.38e−44
p = 5.28e−46
p = 2.85e−46
p = 2.18e−45
p = 1.71e−44
p = 8.71e−44
p = 1.4e−19
p = 2.97e−36
p = 9.78e−37
p = 2.77e−36
p = 1.9e−34
p = 9.96e−34
p = 5.05e−33
p = 2.49e−06
p = 7.44e−10
p = 2.04e−11
p = 5.58e−11
p = 8.96e−12
p = 1.65e−11
p = 1.16e−11
SES_male
SES_S_male
SES_PS_male

b) **Females**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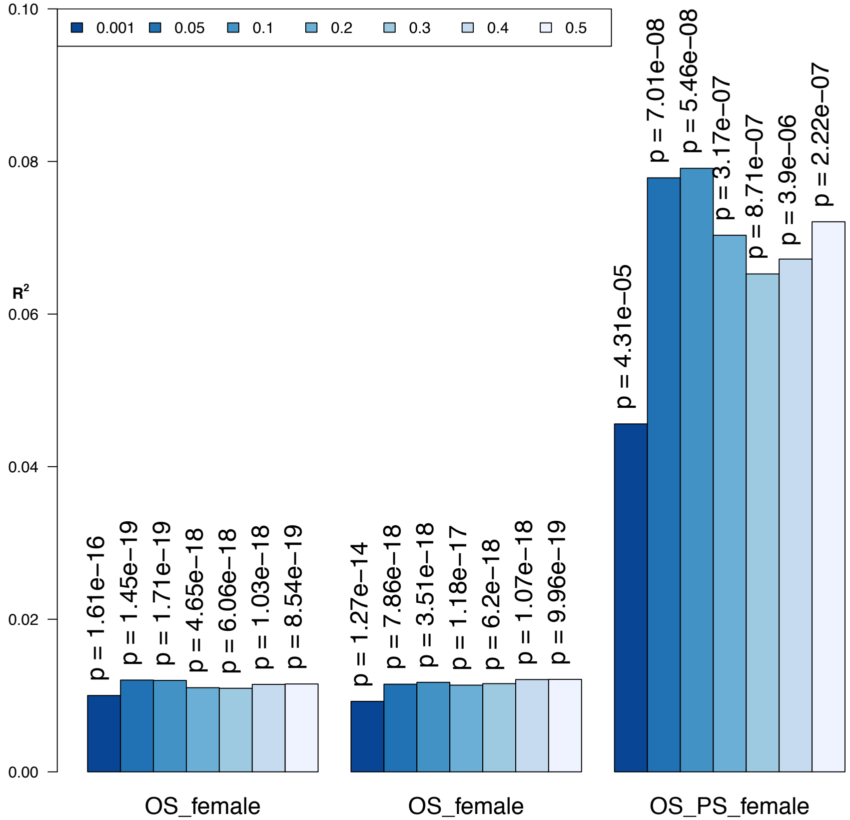
0.05
0.1
0.2
0.3
0.4
0.5
0.08
0.06
0.04
0.02
0.00
R²
p = 2.86e−18
p = 2.08e−22
p = 2.29e−23
p = 4.7e−23
p = 3.27e−22
p = 6.91e−23
p = 3.24e−23
p = 9.47e−16
p = 2.29e−18
p = 4.69e−19
p = 3.87e−18
p = 3.86e−18
p = 9.15e−19
p = 5.5e−19
p = 1.01e−06
p = 5.84e−07
p = 3.4e−07
p = 6.09e−07
p = 9.87e−07
p = 4.45e−07
p = 4.81e−07
EA_female
EA_S_female
EA_PS_female



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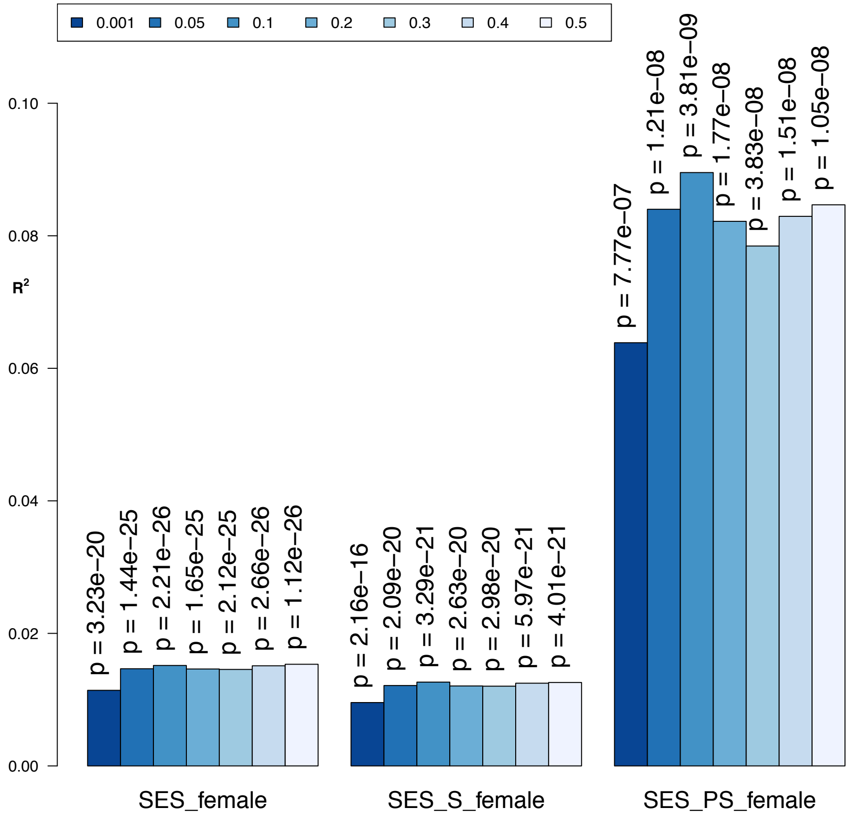
0.05
0.1
0.2
0.3
0.4
0.5
R²
0.10
0.08
0.06
0.04
0.02
0.00
p = 1.61e−16
p = 1.45e−19
p = 1.71e−19
p = 4.65e−18
p = 6.06e−18
p = 1.03e−18
p = 8.54e−19
p = 1.27e−14
p = 7.86e−18
p = 3.51e−18
p = 1.18e−17
p = 6.2e−18
p = 1.07e−18
p = 9.96e−19
p = 4.31e−05
p = 7.01e−08
p = 5.46e−08
p = 3.17e−07
p = 8.71e−07
p = 3.9e−06
p = 2.22e−07
OS_female
OS_female
OS_PS_female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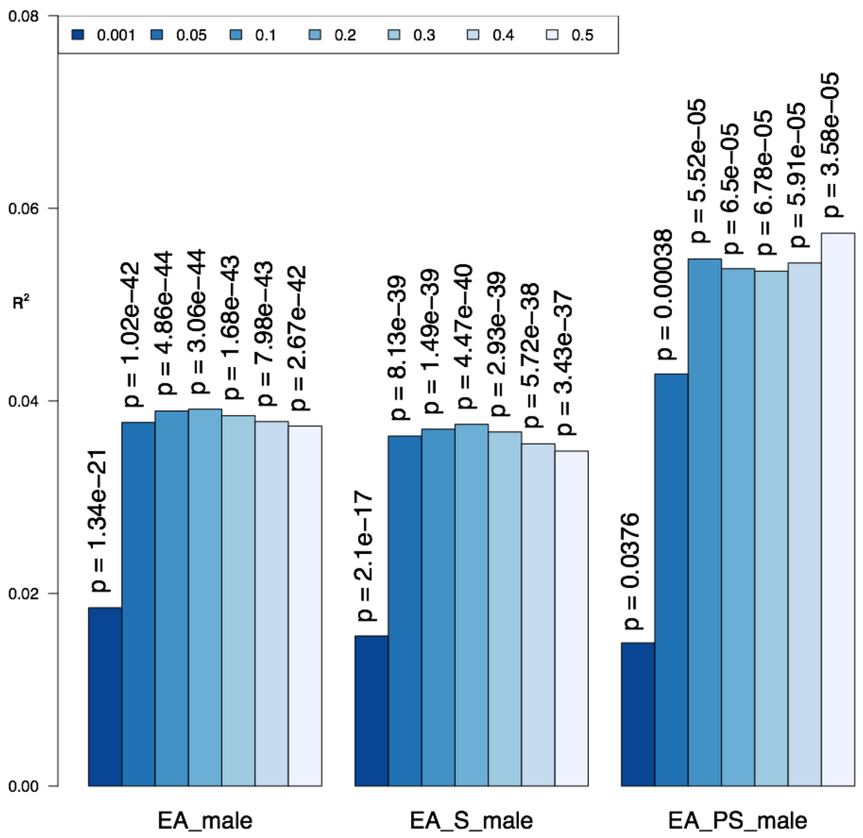
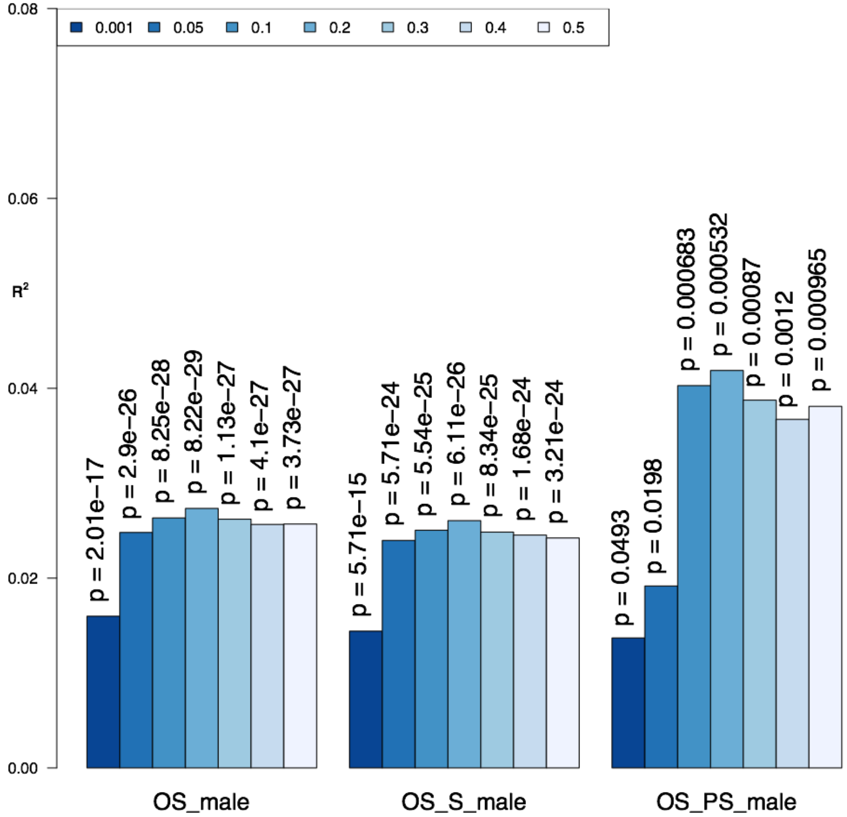
0.1
0.2
0.3
0.4
0.5
0.10
0.08
R²
0.06
0.04
0.02
0.00
p = 3.23e−20
p = 1.44e−25
p = 2.21e−26
p = 1.65e−25
p = 2.12e−25
p = 2.66e−26
p = 1.12e−26
p = 2.16e−16
p = 2.09e−20
p = 3.29e−21
p = 2.63e−20
p = 2.98e−20
p = 5.97e−21
p = 4.01e−21
p = 7.77e−07
p = 1.21e−08
p = 3.81e−09
p = 1.77e−08
p = 3.83e−08
p = 1.51e−08
p = 1.05e−08
SES_female
SES_S_female
SES_PS_female

Males



0.001
0.05
0.1
0.2
0.3
0.4
0.5
0.08
0.06
0.04
0.02
0.00
R^2
p = 1.34e−21
p = 1.02e−42
p = 4.86e−44
p = 3.06e−44
p = 1.68e−43
p = 7.98e−43
p = 2.67e−42
p = 2.1e−17
p = 8.13e−39
p = 1.49e−39
p = 4.47e−40
p = 2.93e−39
p = 5.72e−38
p = 3.43e−37
p = 0.0376
p = 0.00038
p = 5.52e−05
p = 6.5e−05
p = 6.78e−05
p = 5.91e−05
p = 3.58e−05
EA_male
EA_S_male
EA_PS_male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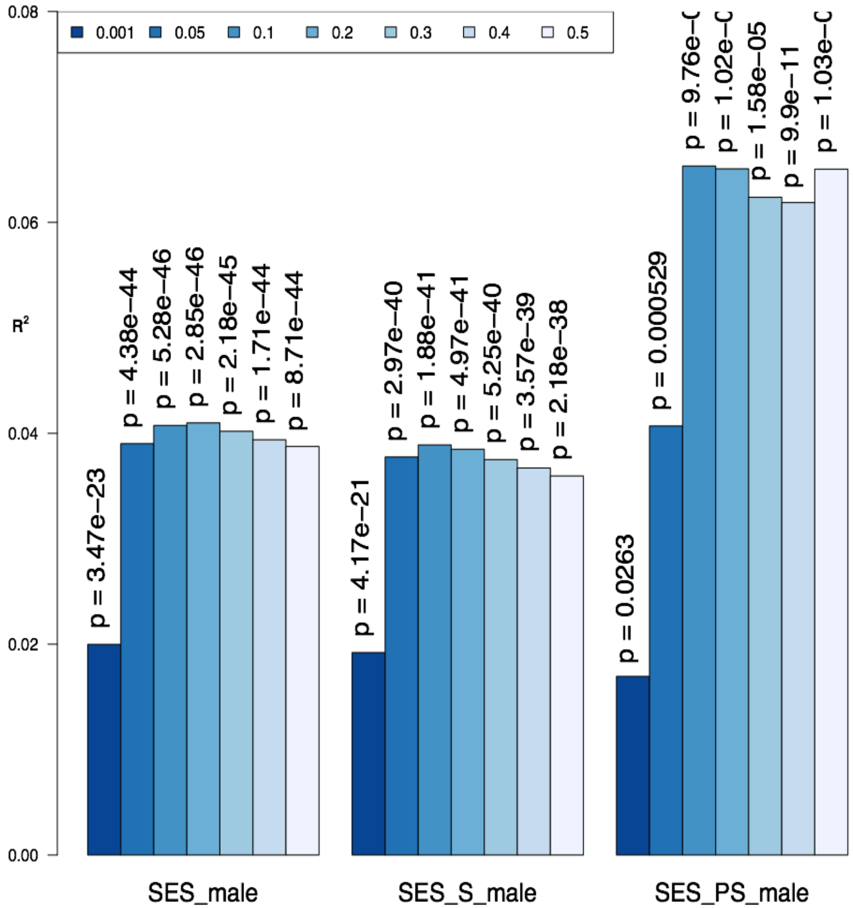
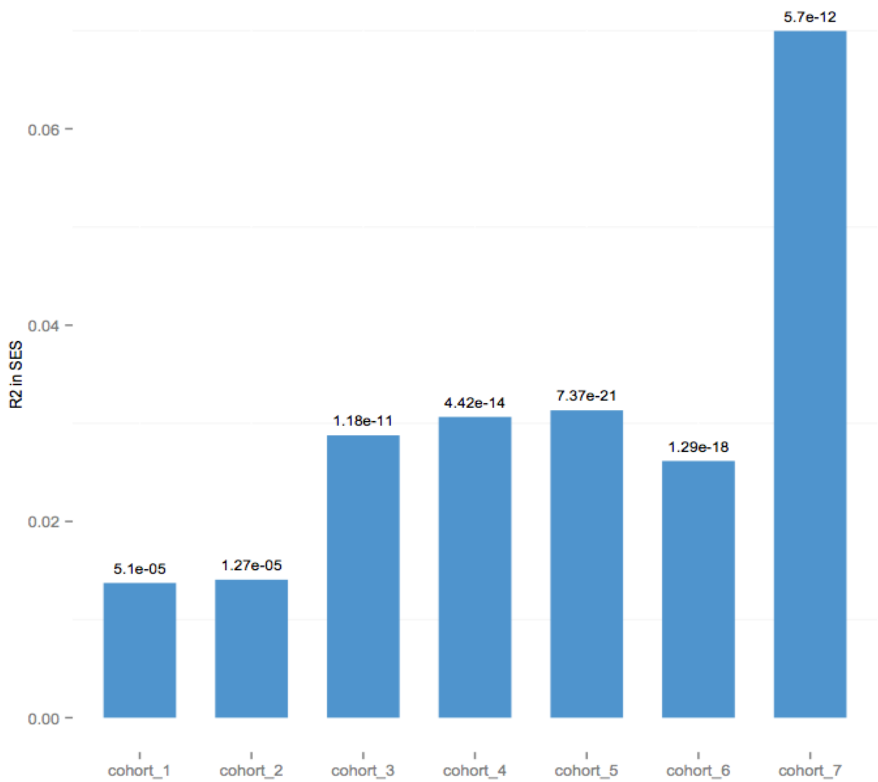
0.3
0.4
0.5
0.08
0.06
0.04
0.02
0.00
R^2
p = 2.01e−17
p = 2.9e−26
p = 8.25e−28
p = 8.22e−29
p = 1.13e−27
p = 4.1e−27
p = 3.73e−27
p = 5.71e−15
p = 5.71e−24
p = 5.54e−25
p = 6.11e−26
p = 8.34e−25
p = 1.68e−24
p = 3.21e−24
p = 0.0493
p = 0.0198
p = 0.000683
p = 0.000532
p = 0.00087
p = 0.0012
p = 0.000965
OS_male
OS_S_male
OS_PS_male


0.08
0.06
0.04
0.02
0.00
R²
0.001
0.05
0.1
0.2
0.3
0.4
0.5
p = 3.47e−23
p = 4.38e−44
p = 5.28e−46
p = 2.85e−46
p = 2.18e−45
p = 1.71e−44
p = 8.71e−44
p = 4.17e−21
p = 2.97e−40
p = 1.88e−41
p = 4.97e−41
p = 5.25e−40
p = 3.57e−39
p = 2.18e−38
p = 0.0263
p = 0.000529
p = 1.58e−05
p = 9.9e−11
SES_male
SES_S_male
SES_PS_male

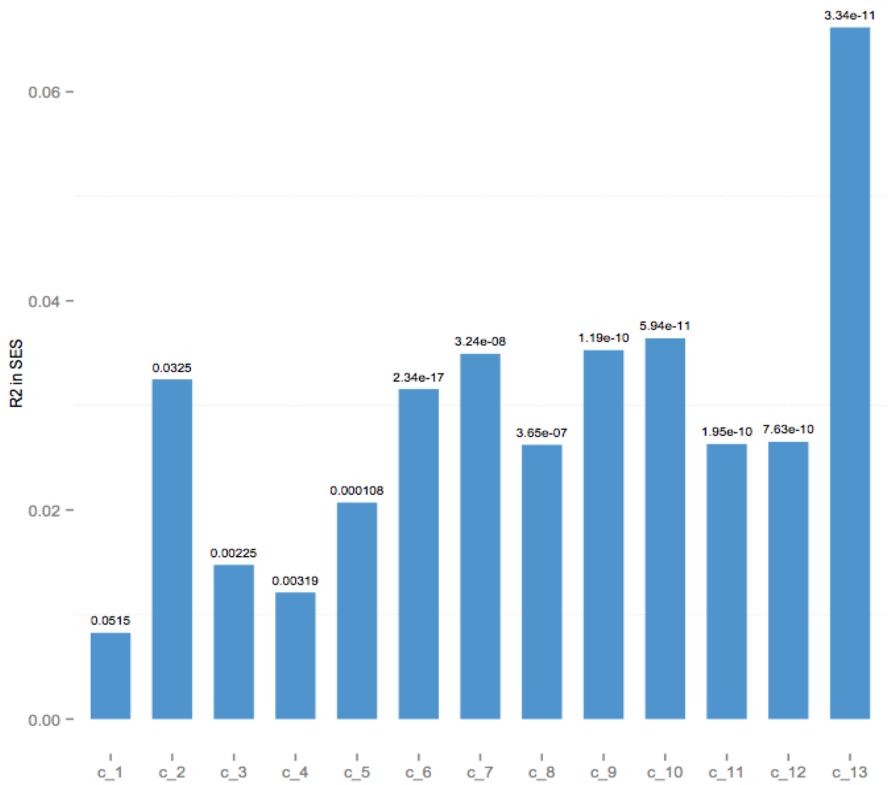
Supplementary Figure 5. GPS heritabilities across birth cohorts for SES p-value threshold of 0.1 for a) birth cohorts across decades and b) birth cohorts when the sample was divided into 5-year intervals.

a) Birth cohorts across decades



Note: cohort 1= born before 1930 (N=1190); cohort 2= born between 1931-1940 (N=1356); cohort 3= born between 1941-1950 (N=1597); cohort 4= born between 1951-1960 (N=1832); cohort 6= born between 1961-1970 (N=2850); cohort 6= born between 1971-1980 (N=3003); cohort 7= born between 1981-1990 (N-675)

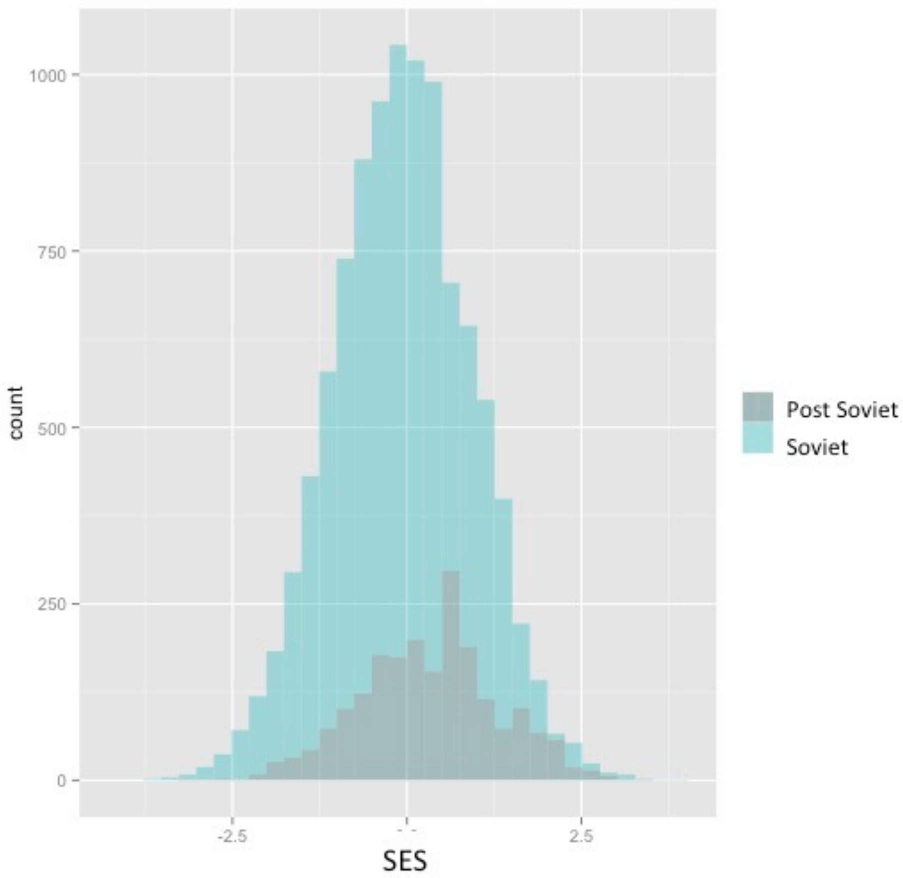
b) Birth cohorts when the sample was divided into 5-year intervals



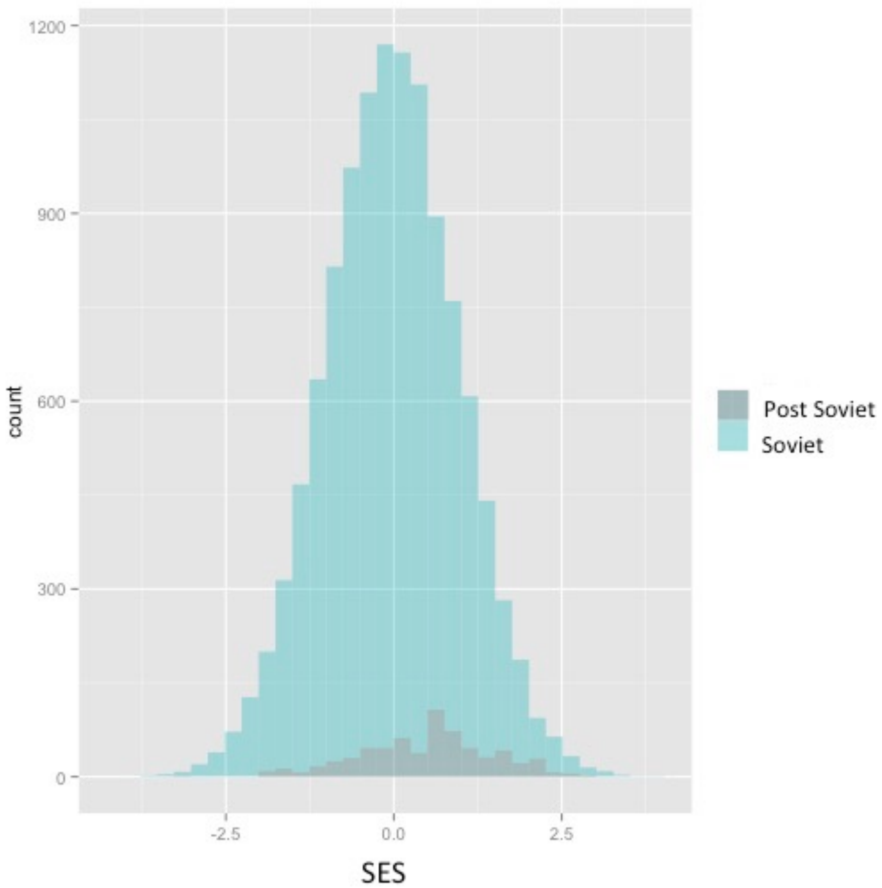
Note: cohort 1= born between 1921-1925 (N=454); cohort 2= born between 1926-1930 (N=579); cohort 3= born between 1931-1935 (N=630); cohort 4= between 1936-1940 (N=715); cohort 5= born between 1941-1945 (N=722); cohort 6= born between 1946-1950 (N=856); cohort 7=born between 1951-1955 (N=864); cohort 8= born between 1956-1960 (N=955); cohort 9= born between 1961-1965 (N=1158); cohort 10= born between 1966-1970 (N=1598); cohort 11= born between 1971-1975 (N=1528); cohort 12= born between 1976-1980 (N=1399) ; cohort 13= born between 1981-1985 (N=647)

Supplementary Figure 6. Distribution of SES for the Soviet and post-Soviet groups using (a) age 15 as a cut-off and (b) age 10 as a cut-off.

a) Age 15 cut-off

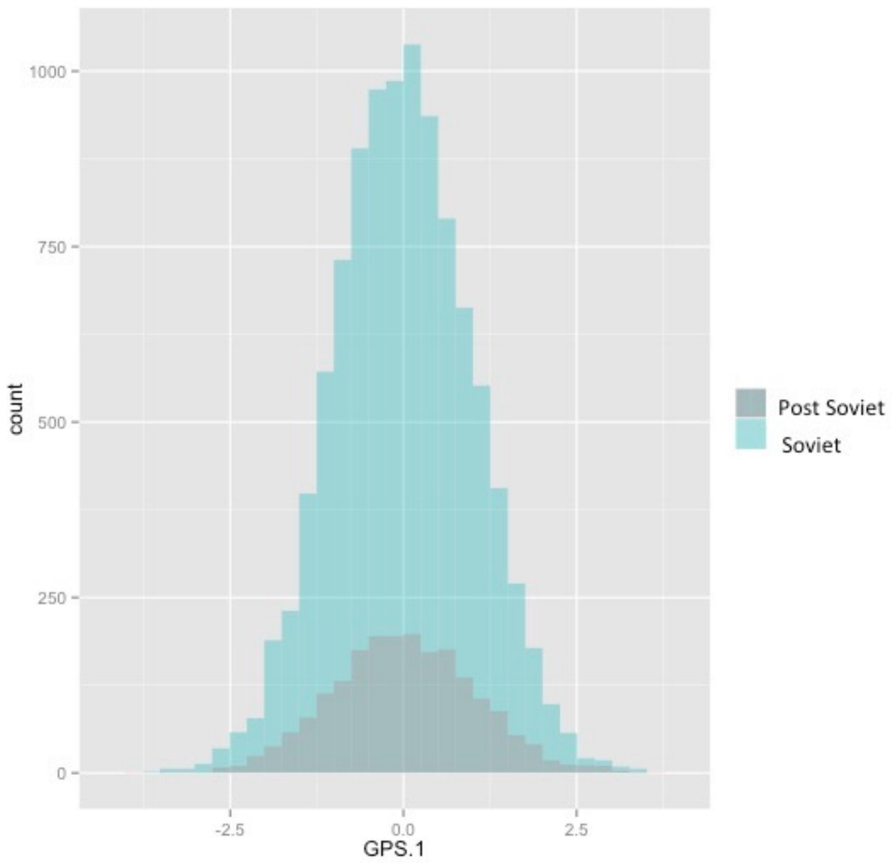


b) Age 10 cut-off

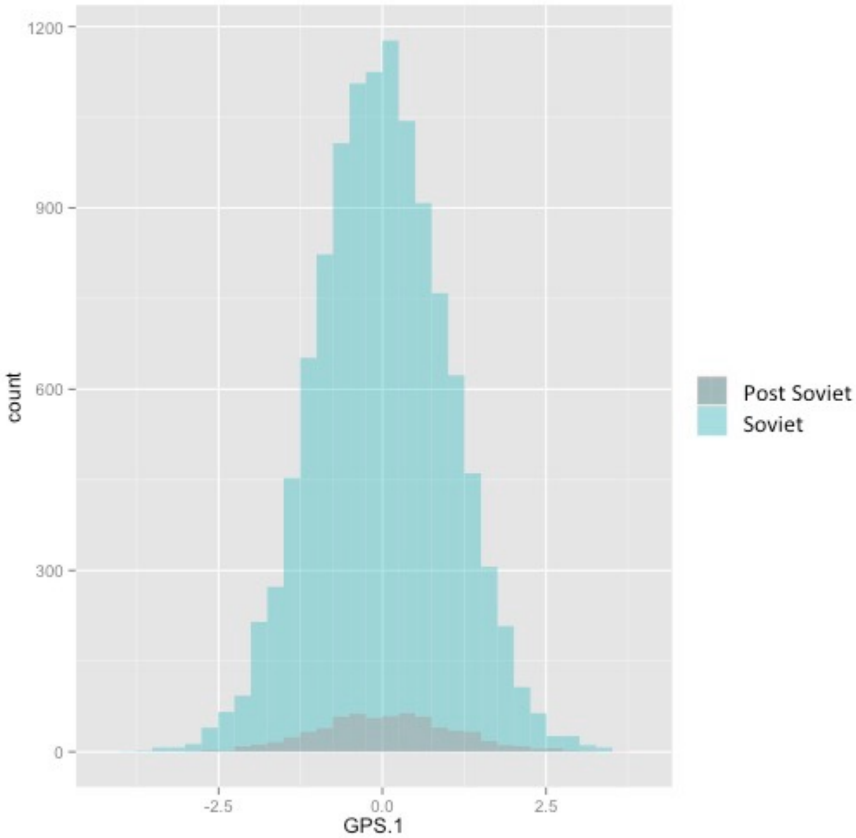


Supplementary Figure 7. Distribution of *EduYears* GPS for the Soviet and post-Soviet groups using (a) age 15 as a cut-off and (b) age 10 as a cut-off.

a) Age 15 cut-off

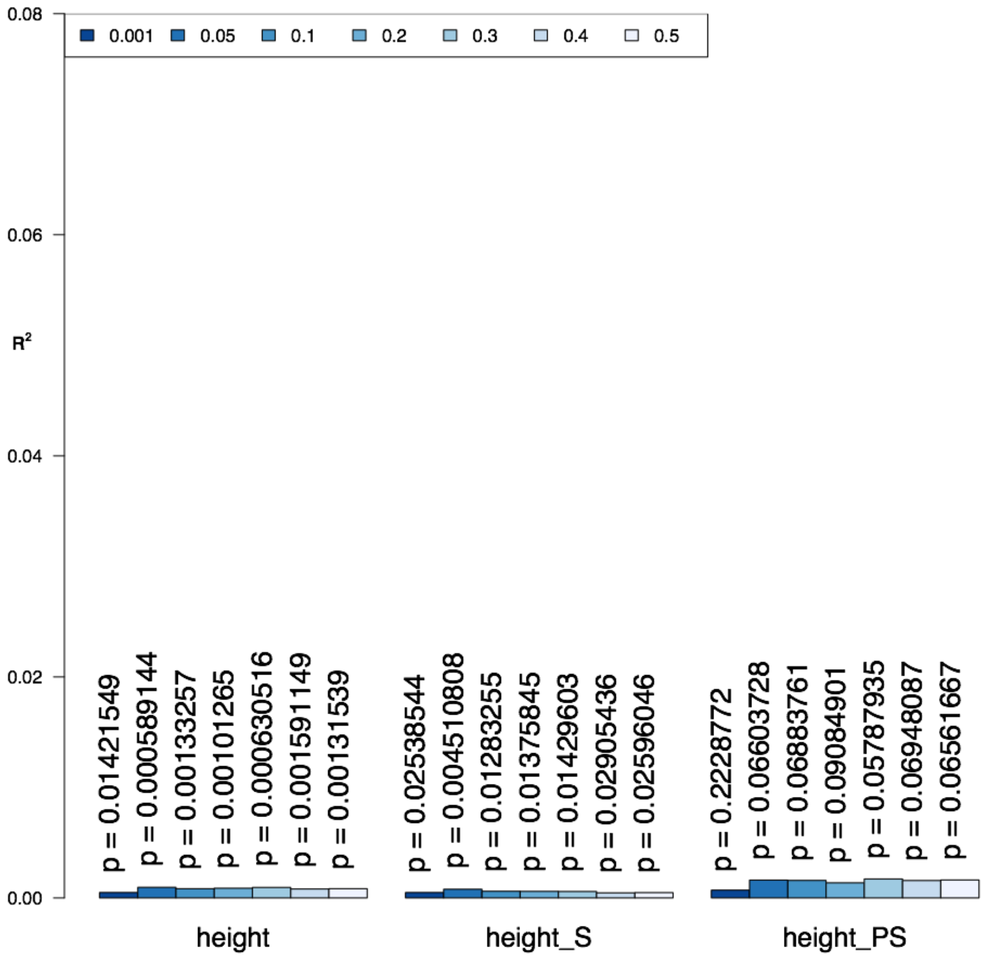


b) Age 10 cut-off

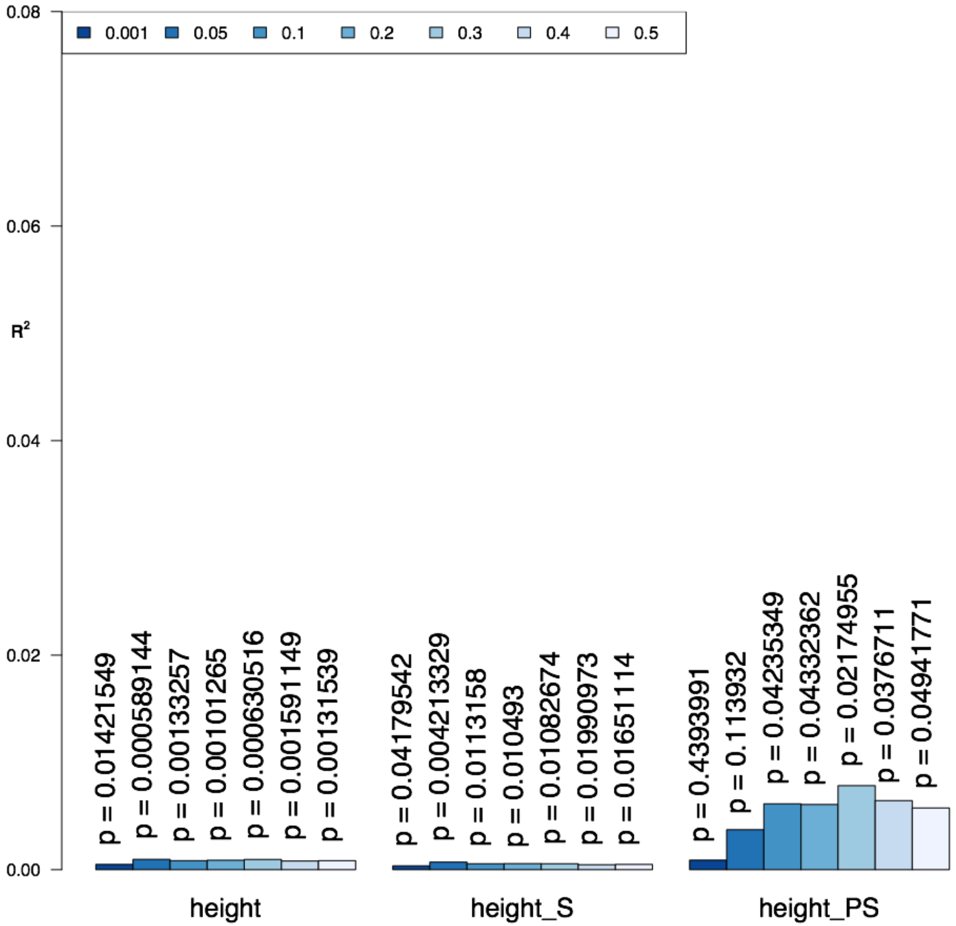


Supplementary Figure 8. GPS heritabilities (*EduYears*) across birth cohorts for height across multiple p-value thresholds for the whole EGCUT sample and for the Soviet (S) and post-Soviet (PS) groups using (a) age 15 as a cut-off and (b) age 10 as a cut-off.

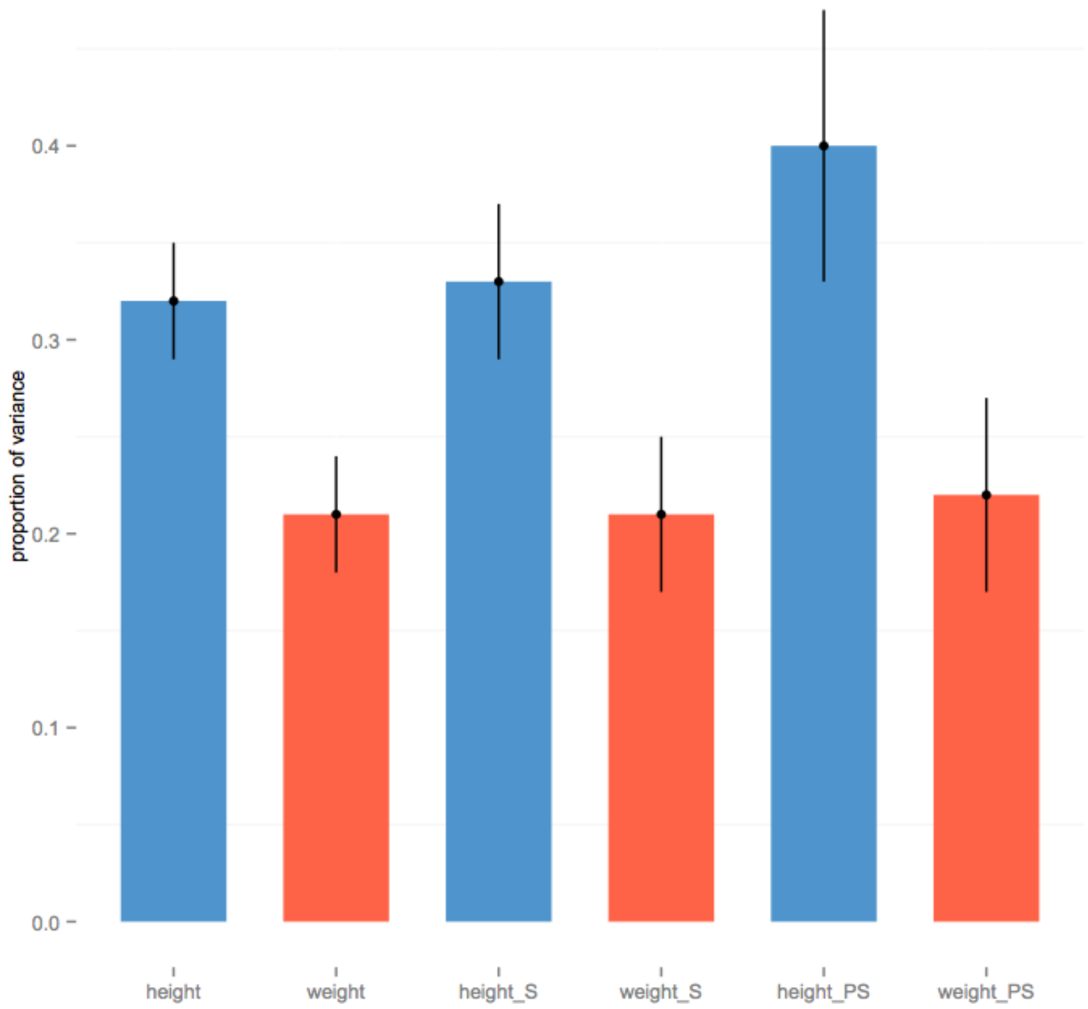
a) Age 15 cut-off



b) Age 10 cut-off

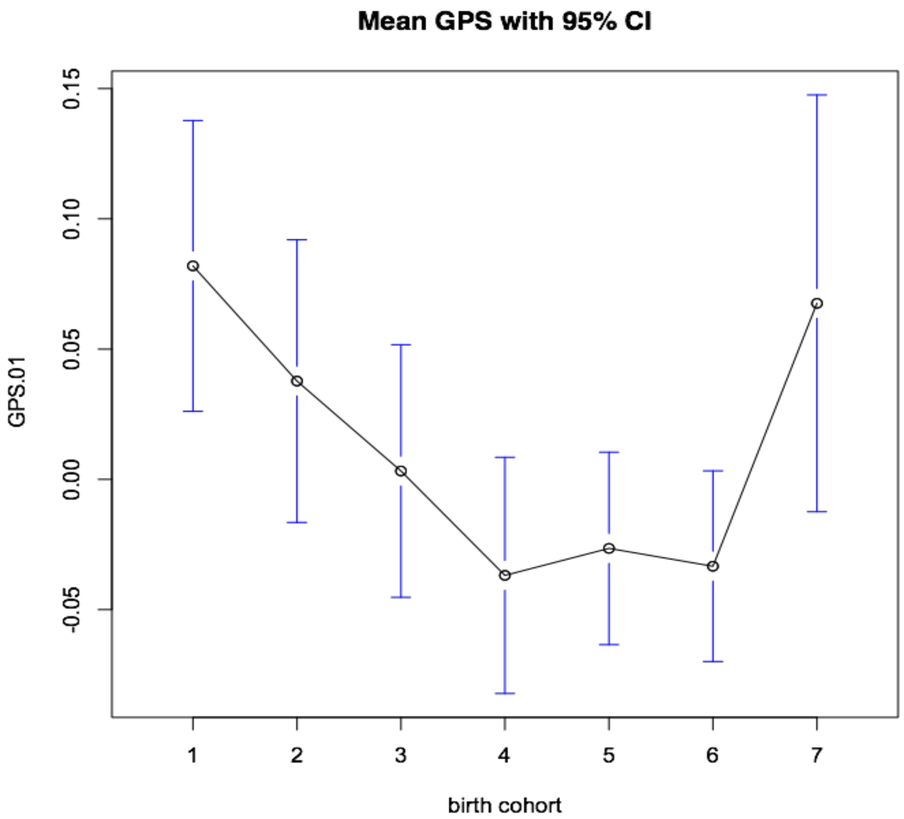


Supplementary Figure 9. SNP heritabilities (SE as error bars) for height and weight for the whole EGCUT sample and for the Soviet (S) and post-Soviet (PS) groups using the age of 15 as a cut-off. SNP heritabilities were adjusted for population stratification.



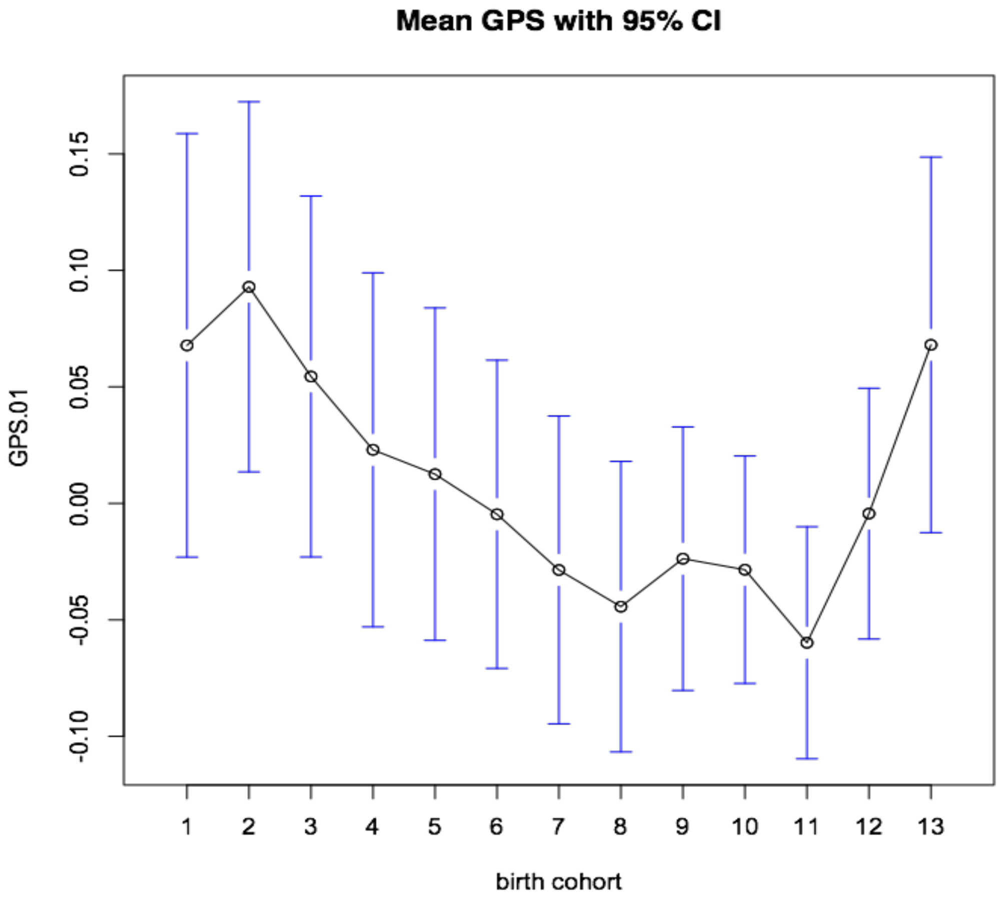
Supplementary Figure 10. Average *EduYears* GPS score (0.1 threshold) with 95% confidence intervals in (a) 10-year birth cohort bins and (b) 5-year birth cohort bins.

a)



Note: cohort 1= born before 1930 (N=1190); cohort 2= born between 1931-1940 (N=1356); cohort 3= born between 1941-1950 (N=1597); cohort 4= born between 1951-1960 (N=1832); cohort 6= born between 1961-1970 (N=2850); cohort 6= born between 1971-1980 (N=3003); cohort 7= born between 1981-1990 (N-675

b)



Note: cohort 1= born between 1921-1925 (N=454); cohort 2= born between 1926-1930 (N=579); cohort 3= born between 1931-1935 (N=630); cohort 4= between 1936-1940 (N=715); cohort 5= born between 1941-1945 (N=722); cohort 6= born between 1946-1950 (N=856); cohort 7=born between 1951-1955 (N=864); cohort 8= born between 1956-1960 (N=955); cohort 9= born between 1961-1965 (N=1158); cohort 10= born between 1966-1970 (N=1598); cohort 11= born between 1971-1975 (N=1528); cohort 12= born between 1976-1980 (N=1399) ; cohort 13= born between 1981-1985 (N=647)

Appendix 2: Supplementary figures and tables for Chapter 3

How specific is second language-learning ability? A twin study exploring the contributions of first language achievement and intelligence to second language achievement

Supplementary Material

Tables

Table S1. Twin intraclass correlations and model fitting estimates for univariate analyses for GCSE language achievement.
Table S2. Phenotypic correlations between GCSE English and intelligence, and the main second languages taken.
Table S3. Correlated factor solution for the trivariate genetic analyses for intelligence, GCSE English and GCSE SL.

Figures

Figure S1. Bivariate model of additive genetic (A), shared environmental (C) and non-shared environmental (E) contributions to the correlations between traits. Two algebraically equivalent representations of the bivariate model are shown: (a) correlated factor solution of genetic correlation (r_G), shared environmental correlation (r_C) and non-shared environmental correlation (r_E) and (b) Cholesky decomposition.

Figure S2. Bivariate model-fitting results for Cholesky decomposition for ‘g’ (intelligence) and GCSE SL with 95% confidence intervals (in parentheses).

Figure S3. Bivariate estimates for intelligence and GCSE second language achievement measures.

Figure S4. Bivariate model-fitting results for Cholesky decomposition for GCSE English and GCSE French, Spanish and German with 95% confidence intervals (in parentheses).

Figure S5. Bivariate model-fitting results for Cholesky decomposition for intelligence and GCSE French, Spanish and German with 95% confidence intervals (in parentheses).

Figure S6. Trivariate model-fitting results for Cholesky decomposition for intelligence (‘g’), GCSE English and GCSE SL.

Table S1.
Twin intraclass correlations and univariate model fitting estimates for additive genetic (A), shared environmental (C) and non-shared environmental (E) components of variance for GCSE language achievement, 95% confidence intervals (in parentheses); N= number of complete twin pairs, MZ=monozygotic, DZ=dizygotic.

	N	**Intraclass correlations**				
		Mz	**Dz**	**A**	**C**	**E**
GCSE SL	2765	0.75	0.47	0.56 (0.48-0.64)	0.20 (0.13-0.27)	0.24 (0.22-0.26)
GCSE French	1323	0.81	0.54	0.53 (0.44-0.63)	0.27(0.18-0.36)	0.20 (0.17-0.21)
GCSE German	450	0.79	0.61	0.36 (0.21-0.52)	0.45 (0.29-0.57)	0.19 (0.16-0.24)
GCSE Spanish	407	0.79	0.50	0.56 (0.38-0.77)	0.22 (0.02-0.39)	0.22 (0.17-0.27)
GCSE English	5911	0.81	0.51	0.62 (0.58-0.67)	0.20 (0.15-0.24)	0.18 (0.17-0.19)

Table S2.

Phenotypic correlations between GCSE English and the main second languages. Correlations calculated on one randomly selected twin per pair. N=number of participants; ** p<.01.

		GCSE English	GCSE French	GCSE German	GCSE Spanish
GCSE English		1			
	N	6030			
GCSE French		0.69**	1		
	N	2112	2113		
GCSE German		0.66**	0.77**	1	
	N	872	157	874	
GCSE Spanish		0.69**	0.75**	0.79**	1
	N	828	207	50	829

Table S3.

Correlated factor solution for the trivariate genetic analyses, demonstrating the phenotypic correlation (r_{Ph}), genetic correlation (r_G), shared-environmental (r_C),non-shared environmental (r_E) correlations, and phenotypic correlations ($r_{ph)}$ between intelligence, GCSE English and GCSE SL, 95% confidence intervals (in parentheses).

***r*G**

	Intelligence	English	SL
Intelligence	1.00		
English	0.64 (0.56-0.74)	1.00	
SL	0.59 (0.59-0.72)	0.82 (0.76-0.87)	1.00

***r*C**

	Intelligence	English	SL
Intelligence	1.00		
English	0.92 (0.46-1.0)	1.00	
SL	0.99 (0.46-1.0)	0.84 (0.71-0.96)	1.00

r_E

	Intelligence	English	SL
Intelligence	1.00		
English	0.19 (0.12-0.26)	1.00	
SL	0.14 (0.05-0.23)	0.22 (0.16-0.28)	1.00

r_{Ph}

	Intelligence	English	SL
Intelligence	1.00		
English	0.52 (0.50-.054)	1.00	
SL	0.48 (0.45-0.51)	0.70 (0.69-0.72)	1.00

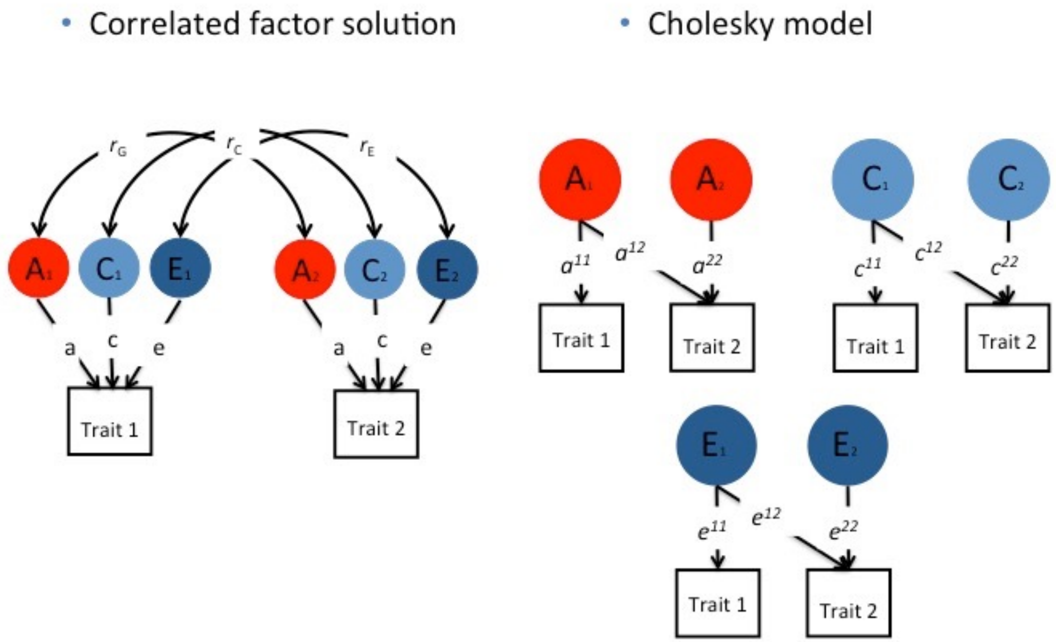


Figure S1.

Bivariate model of additive genetic (A), shared environmental (C) and non-shared environmental (E) contributions to the correlations between traits. Two algebraically equivalent representations of the bivariate model are shown: (a) correlated factor solution of genetic correlation (r_G), shared environmental correlation *(*r_C) and non-shared environmental correlation (r_E) and (b) Cholesky decomposition.

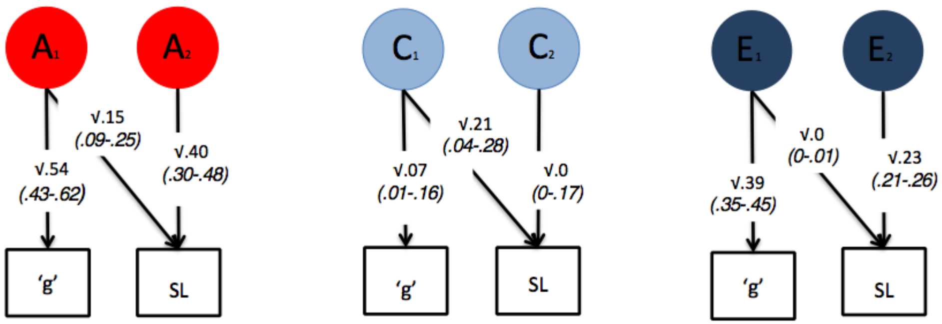


Figure S2.

Bivariate model-fitting results for Cholesky decomposition for 'g' (intelligence) and GCSE SL with 95% confidence intervals (in parentheses).

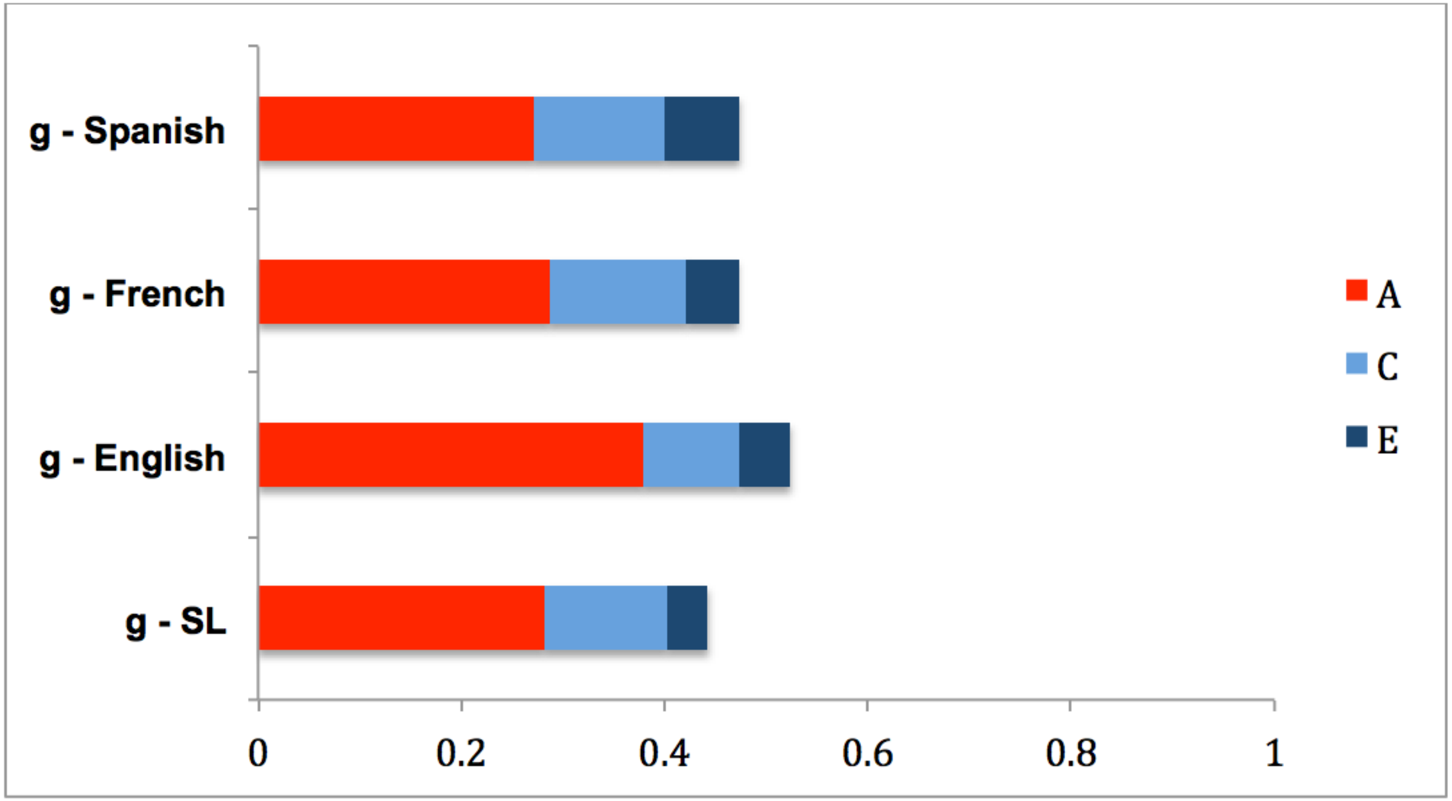
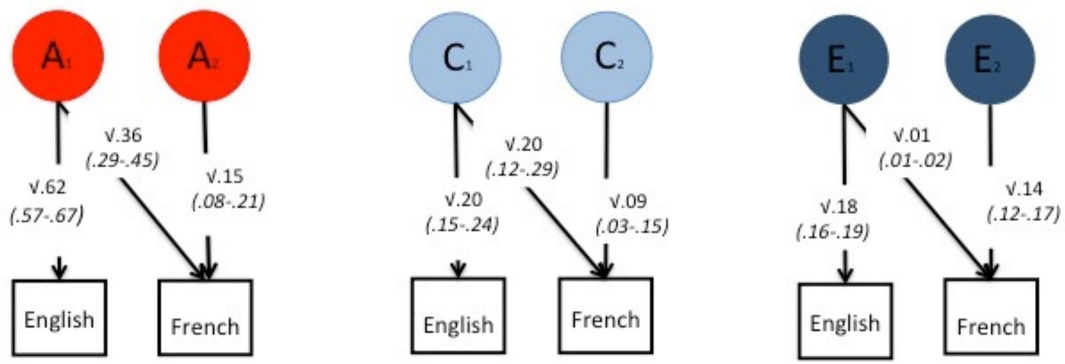
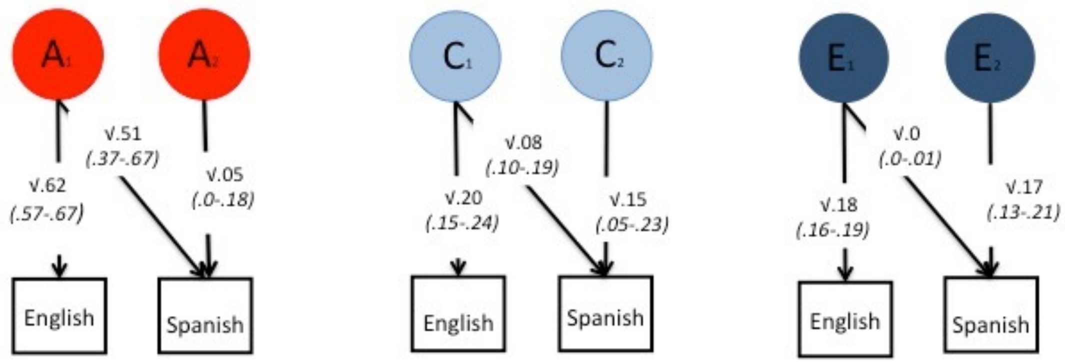


Figure S3.

Bivariate estimates for additive genetic (A), shared environmental (C) and non-shared environmental contributions to the phenotypic correlations between intelligence and GCSE second language achievement measures. Total length of the bar indicates the magnitude of the phenotypic correlation.


A1
A2
√.36
(.29-.45)
√.62
(.57-.67)
√.15
(.08-.21)
English
French
C1
C2
√.20
(.12-.29)
√.20
(.15-.24)
√.09
(.03-.15)
English
French
E1
E2
√.01
(.01-.02)
√.18
(.16-.19)
√.14
(.12-.17)
English
French


A1
A2
√.51
(.37-.67)
√.62
(.57-.67)
√.05
(.0-.18)
English
Spanish
C1
C2
√.08
(.10-.19)
√.20
(.15-.24)
√.15
(.05-.23)
English
Spanish
E1
E2
√.0
(.0-.01)
√.18
(.16-.19)
√.17
(.13-.21)
English
Spanish

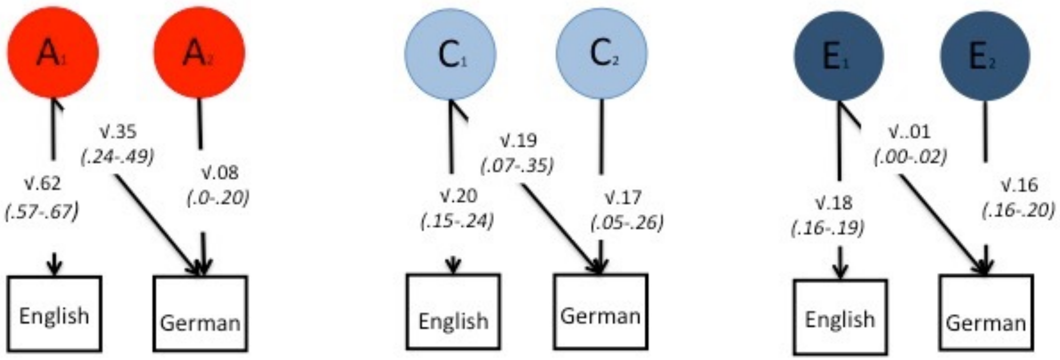
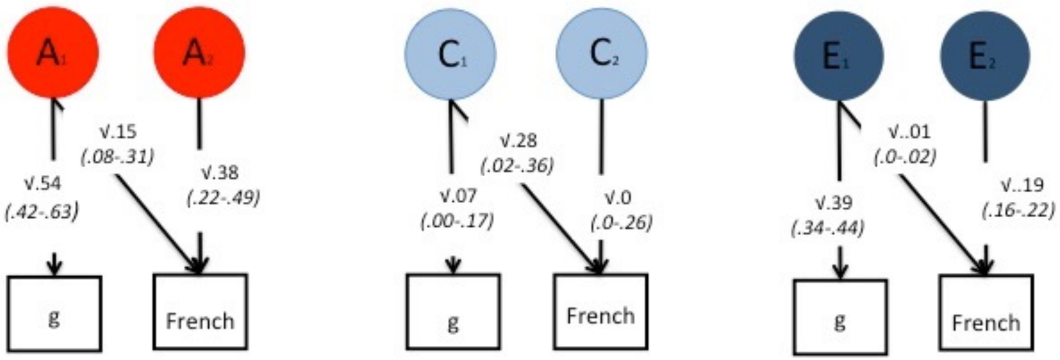
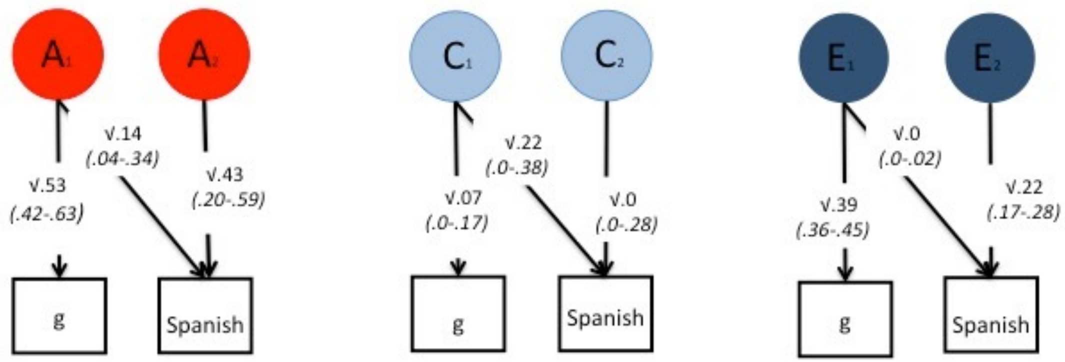


Figure S4.

Bivariate model-fitting results for Cholesky decomposition for GCSE English and GCSE French, Spanish and German with 95% confidence intervals (in parentheses).


A1
A2
√.15
(.08-.31)
√.54
(.42-.63)
√.38
(.22-.49)
g
French
C1
C2
√.28
(.02-.36)
√.07
(.00-.17)
√.0
(.0-.26)
g
French
E1
E2
√..01
(.0-.02)
√.39
(.34-.44)
√..19
(.16-.22)
g
French


A1
A2
√.14
(.04-.34)
√.53
(.42-.63)
√.43
(.20-.59)
g
Spanish
C1
C2
√.22
(.0-.38)
√.07
(.0-.17)
√.0
(.0-.28)
g
Spanish
E1
E2
√.0
(.0-.02)
√.39
(.36-.45)
√.22
(.17-.28)
g
Spanish

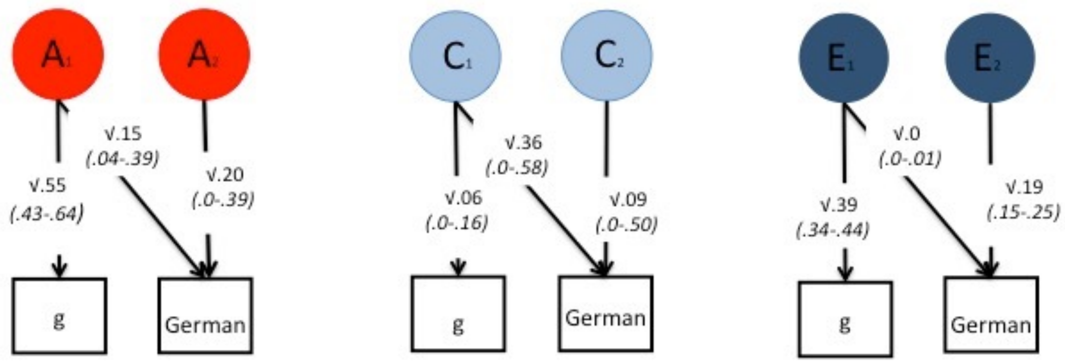
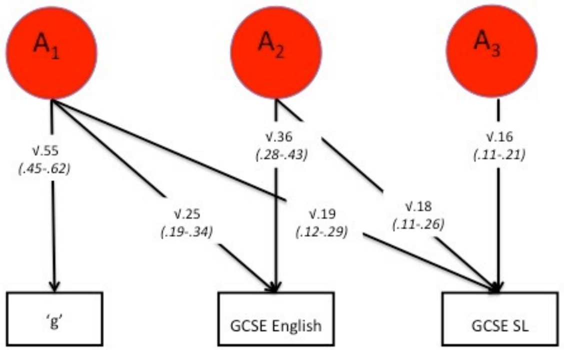
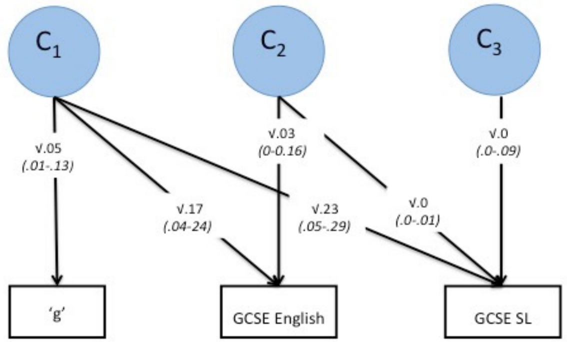


*Figure S5***.**

Bivariate model-fitting results for Cholesky decomposition for intelligence and GCSE French, Spanish and German with 95% confidence intervals (in parentheses).


A_1
A_2
A_3
√.55
(.45-.62)
√.25
(.19-.34)
√.19
(.12-.29)
√.36
(.28-.43)
√.18
(.11-.26)
√.16
(.11-.21)
'g'
GCSE English
GCSE SL


C_1
C_2
C_3
√.05
(.01-.13)
√.17
(.04-24)
√.23
(.05-.29)
√.03
(0-0.16)
√.0
(.0-.01)
√.0
(.0-.09)
'g'
GCSE English
GCSE SL

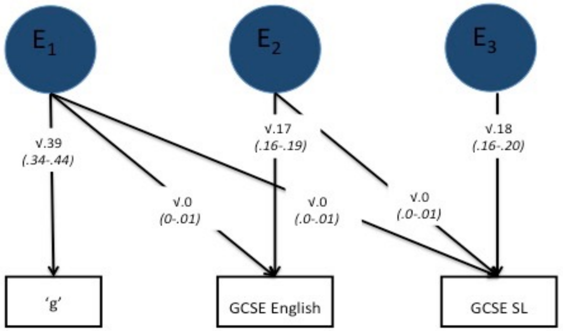


Figure S6.

Trivariate model-fitting results for Cholesky decomposition for intelligence ('g'), GCSE English and GCSE SL with 95% confidence intervals (in parentheses)

Appendix 3: Supplementary figures and tables for Chapter 4

Supplementary information

The high heritability of educational achievement reflects many genetically influenced traits, not just intelligence

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Tables

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Figures

Fig. S1. Bivariate model of additive genetic (A), shared environmental (C), and nonshared environmental (E) contributions to the correlations between traits. Two algebraically equivalent representations of the bivariate model are shown: (A) correlated factor solution of genetic correlation (rG), shared environmental
correlation (rC), and nonshared environmental correlation (rE) and (B) Cholesky decomposition.

Supporting Information

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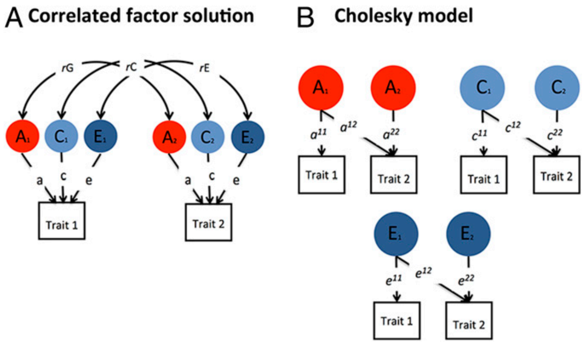

Fig. S1. Bivariate model of additive genetic (A), shared environmental (C), and nonshared environmental (E) contributions to the correlations between traits. Two algebraically equivalent representations of the bivariate model are shown: (*A*) correlated factor solution of genetic correlation (*r*G), shared environmental correlation (*r*C), and nonshared environmental correlation (*r*E) and (*B*) Cholesky decomposition.

Table S1. Descriptive statistics

	N	Whole sample	Male	Female	MZm	DZm	MZf	DZf	DZos	Sex	Zygosity	Sex × zygosity	R^2
GCSE core subjects mean grade	12,103	8.91 (1.23)	8.86 (1.23)	8.96 (1.21)	8.83 (1.23)	8.90 (1.21)	8.95 (1.16)	8.95 (1.24)	8.93 (1.24)	20.26*	1.91	0.13	<0.01

GCSE core subjects mean grade have a maximum of 11 and a minimum of 4, representing grades A* to G. n = sample size after exclusions (individuals). ANOVA performed (one randomly selected twin per pair) to test main and interaction effects of sex and zygosity: results = F statistic. R^2 = proportion of variance explained by sex, zygosity, and their interaction. DZ, dizygotic; f, female; m, male; MZ, monozygotic; os, opposite sex. *P < 0.01.

Table S2. Twin correlations for all nine predictors and GCSE and cross-correlations for all nine predictors with GCSE

	Twin correlations within trait		Cross-correlations with GCSE	
	MZ	DZ	MZ	DZ
GCSE	0.85 (0.83–0.87) n = 2115	0.54 (0.51–0.56) n = 3794		
Intelligence	0.60 (0.55–0.66) n = 760	0.32 (0.27–0.38) n = 1182	0.53 (0.47–0.59) n = 752	0.29 (0.23–0.33) n = 1209
Self-efficacy	0.62 (0.54–0.64) n = 830	0.40 (0.37–0.47) n = 1326	0.40 (0.33–0.45) n = 807	0.21 (0.16–0.26) n = 1316
School environment	0.45 (0.39–0.51) n = 826	0.29 (0.24–0.34) n = 1322	0.32 (0.25–0.38) n = 804	0.16 (0.10–0.21) n = 1314
Home environment	0.54 (0.50–0.62) n = 786	0.33 (0.28–0.39) n = 1233	0.19 (0.11–0.25) n = 766	0.12 (0.07–0.17) n = 1244
Personality	0.64 (0.42–0.55) n = 764	0.21 (0.15–0.26) n = 1188	0.25 (0.18–0.32) n = 752	0.07 (0.01–0.16) n = 1203
Well-being	0.54 (0.48–0.62) n = 704	0.35 (0.29–0.40) n = 1106	0.25 (0.18–0.34) n = 679	0.14 (0.08–0.19) n = 1091
Parent-reported behavior problems	0.87 (0.87–0.91) n = 1661	0.63 (0.60–0.65) n = 1963	0.28 (0.23–0.33) n = 1460	0.16 (0.12–0.19) n = 2568
Child-reported behavior problems	0.48 (0.44–0.53) n = 1639	0.22 (0.18–0.25) n = 1923	0.19 (0.15–0.25) n = 1448	0.10 (0.06–0.14) n = 2547
Health	0.61 (0.57–0.65) n = 1237	0.36 (0.33–0.40) n = 2286	0.10 (0.04–0.16) n = 1103	0.06 (0.01–0.10) n = 1992

DZ, dizygotic; MZ, monozygotic.

Table S3. Model fitting estimates (and 95% CIs) for additive genetic (A), shared environment (C), and nonshared environment (E) components of variance for GCSE and nine predictors

	Variance components (95% CIs)		
	A	C	E
GCSE	0.62 (0.58–0.67)	0.26 (0.21–0.30)	0.12 (0.11–0.13)
Intelligence	0.58 (0.46–0.63)	0.04 (0.01–0.13)	0.39 (0.35–0.43)
Self-efficacy	0.40 (0.30–0.52)	0.21 (0.12–0.30)	0.38 (0.34–0.42)
School environment	0.45 (0.33–0.53)	0.11 (0.05–0.20)	0.44 (0.40–0.49)
Home environment	0.46 (0.33–0.55)	0.09 (0.03–0.20)	0.44 (0.40–0.49)
Personality	0.46 (0.36–0.51)	0.00 (0.00–0.08)	0.53 (0.49–0.58)
Well-being	0.35 (0.22–0.49)	0.17 (0.06–0.28)	0.47 (0.43–0.52)
Parent-reported behavior problems	0.53 (0.49–0.57)	0.36 (0.32–0.40)	0.11 (0.10–0.12)
Child-reported behavior problems	0.48 (0.42–0.51)	0.00 (0.00–0.04)	0.52 (0.49–0.56)
Health	0.48 (0.39–0.57)	0.13 (0.11–0.20)	0.39 (0.36–0.42)

Table S4. Phenotypic correlation matrix between GCSE and nine predictors (with 95% CIs)

	GCSE	Intelligence	Self-efficacy	School environment	Home environment	Personality	Well-being	Parent-reported behavior problems	Child-reported behavior problems	Health
GCSE	1.00									
Intelligence	0.58 (0.56–0.60)	1.00								
Self-efficacy	0.49 (0.46–0.51)	0.35 (0.33–0.38)	1.00							
School environment	0.34 (0.32–0.37)	0.24 (0.21–0.27)	0.46 (0.43–0.48)	1.00						
Home environment	0.17 (0.14–0.20)	0.13 (0.10–0.16)	0.30 (0.28–0.33)	0.52 (0.50–0.55)	1.00					
Personality	0.28 (0.25–0.31)	0.18 (0.15–0.21)	0.42 (0.39–0.45)	0.39 (0.37–0.42)	0.38 (0.36–0.41)	1.00				
Well-being	0.26 (0.23–0.28)	0.17 (0.14–0.20)	0.41 (0.38–0.44)	0.54 (0.52–0.56)	0.61 (0.59–0.63)	0.51 (0.49–0.54)	1.00			
Parent-reported behavior problems	0.33 (0.31–0.35)	0.26 (0.22–0.29)	0.26 (0.22–0.29)	0.29 (0.26–0.33)	0.31 (0.27–0.35)	0.22 (0.18–0.26)	0.38 (0.35–0.41)	1.00		
Child-reported behavior problems	0.25 (0.23–0.27)	0.18 (0.15–0.21)	0.36 (0.33–0.38)	0.39 (0.37–0.42)	0.42 (0.39–0.45)	0.30 (0.27–0.33)	0.54 (0.52–0.56)	0.38 (0.36–0.40)	1.00	
Health	0.08 (0.05–0.12)	0.07 (0.03–0.11)	0.14 (0.10–0.18)	0.23 (0.20–0.27)	0.26 (0.23–0.30)	0.08 (0.04–0.12)	0.32 (0.28–0.35)	0.17 (0.15–0.20)	0.42 (0.40–0.44)	1.00

Table S5. Bivariate model-fitting estimates (and CIs)

	Proportion of phenotypic correlation explained by A, C, and E (95% CIs)		
	A	C	E
Intelligence-GCSE	0.75 (0.63–0.86)	0.15 (0.06–0.26)	0.10 (0.07–0.13)
Self-efficacy-GCSE	0.64 (0.51–0.77)	0.21 (0.09–0.33)	0.15 (0.11–0.18)
School environment-GCSE	0.59 (0.37–0.80)	0.31 (0.12–0.50)	0.10 (0.04–0.16)
Home environment-GCSE	0.08 (-0.35–0.50)	0.81 (0.44–1.18)	0.10 (-0.01–0.26)
Personality-GCSE	0.92 (0.66–1.17)	(-0.05) (-0.27–0.17)	0.14 (0.06–0.21)
Well-being-GCSE	0.53 (0.22–0.85)	0.34 (0.06–0.61)	0.13 (0.04–0.21)
Parent-reported behavior problems-GCSE	0.81 (0.70–0.93)	0.11(-4.25E-03–0.22)	0.07 (0.06–0.10)
Child-reported behavior problems-GCSE	0.89 (0.70–1.08)	(-0.01) (-0.18–0.15)	0.12 (0.12–0.12)
Health-GCSE	0.71 (0.55–1.43)	0.28 (-0.37–0.85)	0.01 (-0.17–0.19)

Bivariate estimates (and 95% CIs) for additive genetic (A), shared environmental (C), and nonshared environmental (E) contributions to the correlations between GCSE and nine predictors.

Table S6. Bivariate model-fitting results of the extent to which the heritability of GCSE can be explained by the nine predictors (95% CIs)

	Heritability of GCSE	
	Shared	Independent
Intelligence	0.31 (0.22–0.37)	0.31 (0.25–0.41)
Self-efficacy	0.23 (0.15–0.33)	0.39 (0.15–0.32)
School environment	0.12 (0.05–0.25)	0.50 (0.37–0.59)
Home environment	0.00 (6E-18–0.02)	0.63 (6E-01–0.02)
Personality	0.13 (7E-02–0.22)	0.50 (4E-01–0.58)
Well-being	0.05 (0.01–0.12)	0.58 (0.50–0.65)
Parent-reported behavior problems	0.13 (0.13–0.16)	0.50 (0.44–0.54)
Child-reported behavior problems	1E-01 (6E-02–0.15)	5E-01 (6E-02–0.15)
Health	0.01 (5E-05–0.03)	0.62 (6E-01–0.67)

The graph displays the decomposition of heritability of GCSE into shared variance accounted for by genetic influences on the respective domain and independent variance, which is residual (i.e., unaccounted by the respective domain). As an example, for intelligence, the genetic loading of 0.31 on GCSE, estimated for the squared path a^{21} (Fig. 4), indicates that genetic influences on intelligence accounted for ~50% of the heritability of GCSE.

Table S7. Phenotypic multivariate Cholesky and genetic multivariate Cholesky model-fitting estimates (and 95% CIs) for all nine predictors

	Phenotypic variance of GCSE		Heritability of GCSE	
Predictors of GCSE	Shared	Independent	Shared	Independent
Intelligence	0.34 (0.30–0.38)	0.66 (0.63–0.70)	0.31 (0.25–0.41)	0.31 (0.22–0.37)
Eight noncognitive predictors	0.28	0.72 (0.69–0.76)	0.30	0.31 (3E-16–0.38)
Eight noncognitive predictors and intelligence	0.45	0.55 (0.52–0.58)	0.45	0.15 (6E-16–0.24)

Decomposition of the phenotypic variance and of heritability of GCSE into shared variance accounted for by phenotypic or genetic influences on the respective predictors and independent variance, which is residual (i.e., unaccounted by the respective predictors). As an example, the eight noncognitive predictors alone account for 28% (0.28/1.0) of the phenotypic variance in GCSE and 49% (0.30/0.61) of the heritability of GCSE, leaving 72% (0.72/1.0) phenotypic and 51% (0.31/0.61) residual GCSE heritability. For the models with multiple predictors (i.e., eight noncognitive predictors and intelligence), the shared variance represents the sum of the GCSE variance/heritability explained by all predictors together. Hence, CIs cannot be computed for these summed estimates, but only for the independent GCSE variance/heritability or single predictors (i.e., intelligence).

Table S8. Genetic (*r*G) correlation matrices between the GCSE composite and the nine predictor composites (with 95% CIs)

	Genetic correlations (*r*G)									
	GCSE	Intelligence	Self-efficacy	School environment	Home environment	Personality	Well-being	Parent-reported behavior problems	Child-reported behavior problems	Health
GCSE	1.00									
Intelligence	0.76 (0.68–0.84)	1.00								
Self-efficacy	0.62 (0.52–0.73)	0.64 (0.49–0.81)	1.00							
School environment	0.43 (0.30–0.60)	0.40 (0.22–0.61)	0.62 (0.43–0.81)	1.00						
Home environment	0.10 (−0.02–0.21)	0.08 (−0.09–0.23)	0.25 (0.06–0.41)	0.53 (0.35–0.69)	1.00					
Personality	0.47 (0.35–0.61)	0.29 (0.15–0.43)	0.58 (0.42–0.72)	0.63 (0.46–0.82)	0.55 (0.41–0.69)	1.00				
Well-being	0.29 (0.17–0.42)	0.24 (0.07–0.41)	0.47 (0.29–0.65)	0.65 (0.49–0.83)	0.78 (0.66–0.89)	0.68 (0.55–0.83)	1.00			
Parent-reported behavior problems	0.46 (0.40–0.51)	0.36 (0.24–0.48)	0.43 (0.30–0.56)	0.44 (0.27–0.63)	0.35 (0.22–0.49)	0.30 (0.16–0.45)	0.35 (0.23–0.48)	1.00		
Child-reported behavior problems	0.39 (0.30–0.48)	0.25 (0.11–0.39)	0.57 (0.43–0.75)	0.70 (0.55–0.93)	0.55 (0.43–0.67)	0.45 (0.32–0.58)	0.74 (0.63–0.84)	0.45 (0.38–0.53)	1.00	
Health	0.09 (−0.01–0.19)	0.09 (−0.08–0.29)	0.13 (−0.09–0.36)	0.28 (0.01–0.56)	0.25 (0.06–0.46)	0.12 (−0.07–0.35)	0.38 (0.19–0.59)	0.15 (0.06–0.23)	0.54 (0.44–0.66)	1.00

Derived from the standardized multivariate Cholesky (correlated factors solution).

Table S9. Shared environmental (*r*C) correlation matrices between the GCSE composite and the nine predictor composites (with 95% CIs)

	Shared environment correlations (*r*C)									
	GCSE	Intelligence	Self-efficacy	School environment	Home environment	Personality	Well-being	Parent-reported behavior problems	Child-reported behavior problems	Health
GCSE	1.00									
Intelligence	0.65 (0.40–0.87)	1.00								
Self-efficacy	0.47 (0.28–0.65)	(−0.09) (−0.48–0.27)	1.00							
School environment	0.62 (0.32–0.98)	0.28 (−0.27–0.80)	0.55 (0.19–0.89)	1.00						
Home environment	0.66 (0.34–0.92)	0.49 (−0.04–0.86)	0.66 (0.31–0.90)	0.85 (0.39–1.00)	1.00					
Personality	(−0.03) (0.94–0.86)	0.09 (−0.97–0.91)	0.48 (−0.76–0.99)	0.48 (−0.81–0.99)	0.67 (−0.58–1.00)	1.00				
Well-being	0.46 (0.18–0.72)	0.13 (−0.31–0.63)	0.40 (0.05–0.67)	0.81 (0.39–0.98)	0.75 (0.40–0.95)	0.49 (−0.56–1.00)	1.00			
Parent-reported behavior problems	0.16 (0.04–0.27)	0.25 (−0.05–0.54)	0.09 (−0.13–0.28)	0.41 (0.12–0.76)	0.57 (0.28–0.82)	0.61 (−0.19–1.00)	0.79 (0.56–0.96)	1.00		
Child-reported behavior problems	0.19 (−0.18–0.54)	0.12 (−0.45–0.68)	0.52 (0.01–0.81)	0.63 (−0.04–0.95)	0.83 (0.42–0.98)	0.81 (−0.26–1.00)	0.80 (0.41–0.98)	0.80 (0.52–0.99)	1.00	
Health	0.17 (−0.09–0.45)	0.32 (−0.26–0.81)	0.45 (0.01–0.86)	0.43 (−0.28–0.91)	0.74 (0.13–0.98)	0.65 (−0.57–1.00)	0.33 (−0.16–0.76)	0.38 (0.20–0.62)	0.77 (0.25–0.98)	1.00

Derived from the standardized multivariate Cholesky (correlated factors solution).

Table S10. Nonshared environmental (rE) correlation matrices between the GCSE composite and the nine predictor composites (with 95% CIs)

	Nonshared environmental correlations (rE)									
	GCSE	Intelligence	Self-efficacy	School environment	Home environment	Personality	Well-being	Parent-reported behavior problems	Child-reported behavior problems	Health
GCSE	1.00									
Intelligence	0.24 (0.17–0.31)	1.00								
Self-efficacy	0.31 (0.24–0.37)	0.21 (0.15–0.28)	1.00							
School environment	0.13 (0.07–0.20)	0.09 (0.03–0.16)	0.31 (0.25–0.36)	1.00						
Home environment	0.05 (−0.02–0.13)	0.10 (0.03–0.17)	0.23 (0.17–0.30)	0.45 (0.40–0.50)	1.00					
Personality	0.14 (0.06–0.21)	0.08 (0.20–0.15)	0.33 (0.27–0.39)	0.24 (0.18–0.30)	0.23 (0.16–0.29)	1.00				
Well-being	0.10 (0.03–0.17)	0.12 (0.05–0.18)	0.36 (0.30–0.42)	0.39 (0.33–0.44)	0.43 (0.37–0.48)	0.41 (0.35–0.46)	1.00			
Parent-reported behavior problems	0.20 (0.15–0.25)	0.12 (0.04–0.20)	0.20 (0.12–0.28)	0.09 (0.02–0.17)	0.13 (0.05–0.22)	0.09 (0.01–0.17)	0.19 (0.11–0.26)	1.00		
Child-reported behavior problems	0.12 (0.06–0.17)	0.13 (0.06–0.20)	0.16 (0.09–0.22)	0.15 (0.09–0.22)	0.26 (0.19–0.32)	0.15 (0.06–0.24)	0.35 (0.30–0.41)	0.27 (0.22–0.31)	1.00	
Health	0.00 (−0.06–0.06)	(−0.04) (−0.13–0.05)	0.02 (−0.08–0.11)	0.14 (0.05–0.23)	0.15 (0.06–0.24)	(−0.02) (−0.11–0.07)	0.25 (0.17–0.33)	0.07 (0.02–0.12)	0.27 (0.22–0.31)	1.00

Derived from the standardized multivariate Cholesky (correlated factors solution).

Appendix 4: Supplementary tables for Chapter 6

Supplementary Information

Genetics affects choice of academic subjects as well as achievement

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Tables

Supplementary Table 1. Sex limitation model fitting sub-model comparisons

Supplementary Table 2. Sex limitation model fitting results, showing A,C,E, estimates separately for males and females. A-additive genetic; C- shared environmental; E- non-shared environmental proportions of the variance (95% confidence intervals)

Supplementary Table 3. Model fitting results for liability threshold analyses for A-level choice with twin tetrachoric correlations (N of twin pairs). A-additive genetic; C- shared environmental; E- non-shared environmental proportions of the variance (95% confidence intervals)

Supplementary Table 4. Model fitting results for univariate analyses for A-level exam achievement with twin intraclass correlations (N of complete pairs). A-additive genetic; C- shared environmental; E- non-shared environmental proportions of the variance (95% confidence intervals)

Supplementary Table 1. Sex limitation model fitting sub-model comparisons

A-level mean grade

Qualitative genetic differences							
Model	ep	-2LL	df	AIC	diffLL	diffdf	p
FullHetACE	9	16545.85	6067	4411.85	-	-	-
HetACE	8	16546.29	6068	4410.29	0.45	1	0.5
Qualitative environmental differences							
Model	ep	-2LL	df	AIC	diffLL	diffdf	p
cFullHetACE	9	16545.85	6067	4411.85	-	-	-
HetACE	8	16546.29	6068	4410.29	0.45	1	0.5
Quantitative genetic differences							
Model	ep	-2LL	df	AIC	diffLL	diffdf	p
HetACE	8	16546.29	6068	4410.29	-	-	-
HomACE	5	16561.16	6071	4419.16	14.86	3	0

Qualitative genetic differences

Model	ep	-2LL	df	AIC	diffLL	diffdf	p
FullHetACE	9	7164.26	2586	1992.26	-	-	-
HetACE	8	7164.26	2587	1990.26	0	1	0.97

Qualitative environmental differences

Model	ep	-2LL	df	AIC	diffLL	diffdf	p
cFullHetACE	9	7164.26	2586	1992.26	-	-	-
HetACE	8	7164.26	2587	1990.26	0	1	0.97

Quantitative genetic differences

Model	ep	-2LL	df	AIC	diffLL	diffdf	p
HetACE	8	7164.26	2587	1990.26	-	-	-
HomACE	5	7176.78	2590	1996.78	12.53	3	0.01

Qualitative genetic differences							
Model	ep	-2LL	df	AIC	diffLL	diffdf	p
FullHetACE	9	9366.22	3399	2568.22	-	-	-
HetACE	8	9366.27	3400	2566.27	0.05	1	0.82
Qualitative environmental differences							
Model	ep	-2LL	df	AIC	diffLL	diffdf	p
cFullHetACE	9	9366.22	3399	2568.22	-	-	-
HetACE	8	9366.27	3400	2566.27	0.05	1	0.82
Quantitative genetic differences							
Model	ep	-2LL	df	AIC	diffLL	diffdf	p
HetACE	8	9366.27	3400	2566.27	-	-	-
HomACE	5	9372.89	3403	2566.89	6.61	3	0.09

Qualitative genetic differences							
Model	ep	-2LL	df	AIC	diffLL	diffdf	p
FullHetACE	9	5497.6	1993	1511.6	-	-	-
HetACE	8	5497.95	1994	1509.95	0.35	1	0.55
Qualitative environmental differences							
Model	ep	-2LL	df	AIC	diffLL	diffdf	p
cFullHetACE	9	5498.73	1993	1512.73	-	-	-
HetACE	8	5497.95	1994	1509.95	-0.79	1	1
Quantitative genetic differences							
Model	ep	-2LL	df	AIC	diffLL	diffdf	p
HetACE	8	5497.95	1994	1509.95	-	-	-
HomACE	5	5518.38	1997	1524.38	20.43	3	0

Qualitative genetic differences

Model	ep	-2LL	df	AIC	diffLL	diffdf	p
FullHetACE	9	4481.7	1625	1231.7	-	-	-
HetACE	8	4481.91	1626	1229.91	0.21	1	0.64

Qualitative environmental differences

Model	ep	-2LL	df	AIC	diffLL	diffdf	p
cFullHetACE	9	4481.7	1625	1231.7	-	-	-
HetACE	8	4481.91	1626	1229.91	0.21	1	0.64

Quantitative genetic differences

Model	ep	-2LL	df	AIC	diffLL	diffdf	p
HetACE	8	4481.91	1626	1229.91	-	-	-
HomACE	5	4490.56	1629	1232.56	8.65	3	0.03

Qualitative genetic differences							
Model	ep	-2LL	df	AIC	diffLL	diffdf	p
FullHetACE	9	2319.59	837	645.59	-	-	-
HetACE	8	2319.81	838	643.81	0.22	1	0.64
Qualitative environmental differences							
Model	ep	-2LL	df	AIC	diffLL	diffdf	p
cFullHetACE	9	2319.52	837	645.52	-	-	-
HetACE	8	2319.81	838	643.81	0.29	1	0.59
Quantitative genetic differences							
Model	ep	-2LL	df	AIC	diffLL	diffdf	p
HetACE	8	2319.81	838	643.81	-	-	-
HomACE	5	2322.17	841	640.17	2.35	3	0.5

Qualitative genetic differences							
Model	ep	-2LL	df	AIC	diffLL	diffdf	p
FullHetACE	9	3472.7	1267	938.7	-	-	-
HetACE	8	3472.7	1268	936.7	0	1	1
Qualitative environmental differences							
Model	ep	-2LL	df	AIC	diffLL	diffdf	p
cFullHetACE	9	3472.7	1267	938.7	-	-	-
HetACE	8	3472.7	1268	936.7	0	1	1
Quantitative genetic differences							
Model	ep	-2LL	df	AIC	diffLL	diffdf	p
HetACE	8	3472.7	1268	936.7	-	-	-
HomACE	5	3483.09	1271	941.09	10.4	3	0.02

Qualitative genetic differences							
Model	ep	-2LL	df	AIC	diffLL	diffdf	p
FullHetACE	9	4980.84	1809	1362.84	-	-	-
HetACE	8	4981.73	1810	1361.73	0.89	1	0.34
Qualitative environmental differences							
Model	ep	-2LL	df	AIC	diffLL	diffdf	p
cFullHetACE	9	4980.77	1809	1362.77	-	-	-
HetACE	8	4981.73	1810	1361.73	0.95	1	0.33
Quantitative genetic differences							
Model	ep	-2LL	df	AIC	diffLL	diffdf	p
HetACE	8	4981.73	1810	1361.73	-	-	-
HomACE	5	4984.88	1813	1358.88	3.15	3	0.37

Qualitative genetic differences							
Model	ep	-2LL	df	AIC	diffLL	diffdf	p
FullHetACE	9	1497.69	544	409.69	-	-	-
HetACE	8	1497.69	545	407.69	0	1	1
Qualitative environmental differences							
Model	ep	-2LL	df	AIC	diffLL	diffdf	p
cFullHetACE	9	1497.69	544	409.69	-	-	-
HetACE	8	1497.69	545	407.69	0	1	1
Quantitative genetic differences							
Model	ep	-2LL	df	AIC	diffLL	diffdf	p
HetACE	8	1497.69	545	407.69	-	-	-
HomACE	5	1499.21	548	403.21	1.52	3	0.68

Qualitative genetic differences

Model	ep	-2LL	df	AIC	diffLL	diffdf	p
FullHetACE	9	3556.09	1279	998.09	-	-	-
HetACE	8	3556.09	1280	996.09	0	1	1

Qualitative environmental differences

Model	ep	-2LL	df	AIC	diffLL	diffdf	p
cFullHetACE	9	3556.09	1279	998.09	-	-	-
HetACE	8	3556.09	1280	996.09	0	1	1

Quantitative genetic differences

Model	ep	-2LL	df	AIC	diffLL	diffdf	p
HetACE	8	3556.09	1280	996.09	-	-	-
HomACE	5	3567.82	1283	1001.82	11.73	3	0.01

Qualitative genetic differences

Model	ep	-2LL	df	AIC	diffLL	diffdf	p
FullHetACE	9	2816.36	1018	780.36	-	-	-
HetACE	8	2816.36	1019	778.36	0	1	1

Qualitative environmental differences

Model	ep	-2LL	df	AIC	diffLL	diffdf	p
cFullHetACE	9	2816.36	1018	780.36	-	-	-
HetACE	8	2816.36	1019	778.36	0	1	1

Quantitative genetic differences

Model	ep	-2LL	df	AIC	diffLL	diffdf	p
HetACE	8	2816.36	1019	778.36	-	-	-
HomACE	5	2820.89	1022	776.89	4.53	3	0.21

Qualitative genetic differences							
Model	ep	-2LL	df	AIC	diffLL	diffdf	p
FullHetACE	9	3371.81	1208	955.81	-	-	-
HetACE	8	3371.81	1209	953.81	0	1	1
Qualitative environmental differences							
Model	ep	-2LL	df	AIC	diffLL	diffdf	p
cFullHetACE	9	3371.81	1208	955.81	-	-	-
HetACE	8	3371.81	1209	953.81	0	1	1
Quantitative genetic differences							
Model	ep	-2LL	df	AIC	diffLL	diffdf	p
HetACE	8	3371.81	1209	953.81	-	-	-
HomACE	5	3376.84	1212	952.84	5.03	3	0.17

Supplementary Table 2. Sex limitation model fitting results, showing A, C, E, estimates separately for males and females. A-additive genetic; C- shared environmental; E- non-shared environmental proportions of the variance (95% confidence intervals)

	Males			**Females**		
Subject	**A**	**C**	**E**	**A**	**C**	**E**
A-level mean grade	0.57 (0.38-0.69)	0.08 (0-0.24)	0.35 (0.31-0.41)	0.52 (0.36-0.69)	0.15 (0-0.29)	0.33 (0.29-0.37)
Humanities mean grade	0.55 (0.18-0.72)	0.09 (0-0.40)	0.36 (0.28-0.48)	0.45 (0.10-0.65)	0.12 (0-0.43)	0.43 (0.35-0.53)
STEM mean grade	0.60 (0.34-0.69)	0.03 (0-0.25)	0.37 (0.31-0.45	0.61 (0.36-0.76)	0.10 (0-0.33)	0.29 (0.24-0.35)
Mathematics mean grade	0.51 (0.15-0.67)	0.08 (0-0.38)	0.41 (0.33-0.52)	0.70 (0.34-0.77)	0.00 (0-0.33)	0.30 (0.23-0.40)
Biology grade	0.23 (0-0.74)	0.46 (0-0.72)	0.31 (0.21-0.46)	0.65 (0.35-0.80)	0.09 (0-0.36)	0.26 (0.19-0.36)
Physics grade	0.36 (0-0.79)	0.37 (0-0.71)	0.27 (0.19-0.40)	0.45 (0-0.82)	0.21 (0-0.75)	0.34 (0.18-0.70)
Chemistry grade	0.76 (0.40-0.85)	0.03 (0-0.35)	0.21 (0.15-0.43)	0.56 (0.17-0.85)	0.23 (0-0.58)	0.21 (0.15-0.31)

English composite grade	0.38 (0-0.80)	0.33 (0-0.72)	0.30 (0.18-0.51)	0.34 (0.04-0.72)	0.40 (0.02-0.66)	0.26 (0.21-0.34)
Second language mean grade	0.82 (0.04-0.94)	0.06 (0-0.74)	0.12 (0.06-0.37)	0.47 (0-0.84)	0.30 (0-0.74)	0.23 (0.15-0.37)
History grade	0.38 (0-0.67)	0.20 (0-0.55)	0.42 (0.27-0.65)	0.10 (0-0.65)	0.56 (0.04-0.73)	0.34 (0.24-0.47)
Geography grade	0.24 (0-0.78)	0.47 (0-0.74)	0.29 (0.18-0.47)	0.63 (0.21-0.80)	0.09 (0-0.44)	0.28 (0.19-0.44)
Psychology grade	0.00 (0-0.72)	0.73 (0-0.84)	0.27 (0.16-0.48)	0.45 (0.07-0.68)	0.14 (0-0.48)	0.41 (0.30-0.56)

Supplementary Table S3. Model fitting results for liability threshold analyses for A-level choice with twin tetrachoric correlations. A-additive genetic; C-shared environmental; E- non-shared environmental proportions of the variance (95% confidence intervals)

				Twin tetrachoric correlations	
Subject choice	**A**	**C**	**E**	**MZ**	**DZ**
A-level	0.44 (0.38-0.51)	0.47 (0.41-0.53)	0.08 (0.07-0.10)	0.92 (0.90-0.93)	0.69 (0.66-0.72)
Humanities composite	0.50 (0.36-0.64)	0.18 (0.07-0.30)	0.31 (0.27-0.36)	0.69 (0.64-0.74)	0.44 (0.38-0.49)
STEM composite	0.60 (0.50-0.71)	0.23 (0.14-0.32)	0.17 (0.14-0.32)	0.83 (0.80-0.86)	0.65 (0.49-0.57)
Mathematics	0.77 (0.65-0.88)	0.08 (0-0.19)	0.15 (0.12-0.18)	0.86 (0.82-0.89)	0.47 (0.41-0.52)
Biology	0.64 (0.47-0.76)	0.07 (0-0.21)	0.29 (0.24-0.35)	0.71 (0.67-0.75)	0.39 (0.34-0.43)
Physics	0.80 (0.65-0.85)	0.00 (0-0.13)	0.20 (0.15-0.26)	0.81 (0.74-0.86)	0.38 (0.29-0.46)
Chemistry	0.57 (0.40-0.74)	0.20 (0.05-0.33)	0.23 (0.18-0.29)	0.77 (0.71-0.82)	0.48 (0.41-0.54)

English composite grade	0.65 (0.57-0.70)	0.00 (0-0.06)	0.35 (0.30-0.41)	0.67 (0.61-0.73)	0.27 (0.20-0.33)
Second language	0.75 (0.52-0.88)	0.09 (0-0.29)	0.17 (0.11-0.23)	0.84 (0.78-0.89)	0.45 (0.35-0.55)
History grade	0.53 (0.33-0.71)	0.13 (0-0.29)	0.34 (0.28-0.41)	0.66 (0.59-0.73)	0.40 (0.33-0.47)
Geography	0.52 (0.29-0.71)	0.13 (0-0.31)	0.35 (0.28-0.43)	0.65 (0.57-0.72)	0.40 (0.32-0.47)
Psychology	0.65 (0.55-0.71)	0 (0-0)	0.35 (0.29-0.41)	0.69 (0.62-0.75)	0.26 (0.17-0.34)

Supplementary Table S4. Model fitting results for univariate analyses for A-level exam achievement with twin intraclass correlations (N of complete pairs). A-additive genetic; C- shared environmental; E- non-shared environmental proportions of the variance (95% confidence intervals)

				Twin intraclass correlations	
Subject	**A**	**C**	**E**	**MZ**	**DZ**
A-level mean grade	0.59 (0.48-0.69)	0.07 (0-0.16)	0.34 (0.31-0.37)	0.64 (1076) (0.60-0.68)	0.36 (1972) (0.32-0.41)
Humanities mean grade	0.49 (0.28-0.66)	0.11 (0-0.29)	0.39 (0.33-0.47)	0.61 (462) (0.53-0.68)	0.36 (815) (0.26-0.45)
STEM mean grade	0.65 (0.49-0.71)	0.02 (0-0.16)	0.33 (0.29-0.38)	0.65 (616) (0.59-0.70)	0.32 (1106) (0.25-0.40)
Mathematics mean grade	0.63 (0.44-0.69)	0.00 (0-0.16)	0.37 (0.31-0.44)	0.63 (364) (0.55-0.70)	0.24 (648) (0.12-0.36)
Biology grade	0.63 (0.37-0.78)	0.11 (0-0.32)	0.27 (0.22-0.35)	0.71 (279) (0.62-0.78)	0.43 (533) (0.29-0.55)
Physics grade	0.49 (0.12-0.78)	0.22 (0-0.54)	0.29 (0.21-0.40)	0.71 (151) (0.57-0.80)	0.51 (292) (0.28-0.68)
Chemistry grade	0.76 (0.49-0.84)	0.03 (0-0.28)	0.21 (0.16-0.28)	0.79 (225) (0.71-0.85)	0.38 (421) (0.22-0.52)

English composite grade	0.54 (0.29-0.77)	0.19 (0-0.41)	0.27 (0.22-0.34)	0.71 (312) (0.62-0.78)	0.45 (592) (0.31-0.57)
Second language mean grade	0.60 (0.20-0.86)	0.20 (0-0.55)	0.21 (0.21-0.31)	0.64 (110) (0.47-0.77)	0.47 (164) (0.15-0.70)
History grade	0.35 (0.03-0.69)	0.29 (0-0.54)	0.36 (0.28-0.48)	0.64 (235) (0.51-0.74)	0.46 (440) (0.29-0.60)
Geography grade	0.49 (0.15-0.78)	0.23 (0-0.51)	0.28 (0.21-0.40)	0.74 (182) (0.61-0.83)	0.49 (312) (0.30-0.64)
Psychology grade	0.45 (0.05-0.71)	0.17 (0-0.51)	0.38 (0.29-0.51)	0.58 (221) (0.43-0.69)	0.39 (379) (0.17-0.57)